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CONCHOLOGY

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C. R. C. PAUL, M.A., PH.D.

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LIMAX GROSSUI LUPU 1970, A SLUG NEW TO THE BRITISH ISLES

JUNE E. CHATFIELD

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(Read before the Society, 18 October 1975)

Abstract: *Limax grossui* Lupu, originally described from Bucharest, is recorded from Ireland where it is widespread. It closely resembles *L. flavus* externally and in having lemon-shaped eggs, but is larger, has rougher tubercles, deeper pigment, an overall green appearance and a more marked pattern of colour blotches on the body and mantle. Internally the spermatheca duct is inserted near the base of the short, broad c-shaped penis in *L. grossui*. *L. flavus* has a long s-shaped penis and the spermatheca duct inserted on the oviduct. The intestinal appendix does not extend as far into the tail in *L. grossui* as it does in *L. flavus*.

L. grossui lives under logs and stones in woodland, while *L. flavus* occurs near human settlement, particularly in crevices of old walls and cellars.

During field work in Ireland in April 1968 with a party of members of the Conchological Society (Kerney, 1968) it was noted that slugs which we had initially recorded as *Limax flavus* L. showed several differences from the form of *L. flavus* with which most of us were familiar in England. The Irish ones were greenish rather than yellow with a marked colour pattern and they were found in woods and under stones often away from human settlement. Nineteen greenish *Limax* were found under a single large stone near the shore of Lough Scur, Co. Leitrim in April 1968 and a few of these were collected for further examination. On dissection the reproductive system was clearly different from that figured by Quick (1960, fig. 14B) for true *Limax flavus* L. On subsequent Conchological Society visits to Ireland (Kerney, 1972, 1973) more greenish *Limax* were recorded: it is probable that *L. grossui* is widespread in Ireland. As a result of the new faunal list being prepared for Europe it became apparent that some decision was needed as to the status of this slug. Thus a short visit was made to Northern Ireland, based at the Ulster Museum, Belfast, in October 1975 to collect some fresh specimens of the green *Limax* for dissection and photography and to check previous observations.

The greenish *Limax* appeared to agree with the description for *Limax grossui* Lupu 1970 in external appearance, anatomy and in the range of habitats in which it was found. As the original description of this species was published in a journal in Roumania not readily available in the British Isles, an outline of the characteristics of *L. grossui* and the ways in which it differs from *L. flavus* is given here. A further paper with additional data on *L. grossui* is in preparation.

EXTERNAL FEATURES

Limax grossui bears a general resemblance to *L. flavus* in external characteristics and also in the lemon shape of the eggs. Externally it may be distinguished by the rougher and larger tubercles on the back of the animal, the deeper pigmentation and the greenish as opposed to yellow overall colour of *L. grossui*. Although there are some blotches on the

body of *L. flavus* due to a variation in the pigmentation, in *L. grossui* the pattern of dark grey-green areas contrasting with paler yellow-green areas is far more marked. The blotches occur both on the dorsal surface of the body and on the mantle shield, but the pigment pattern on the body is not necessarily continuous with that on the mantle. The anterior fringe of the mantle in between grey patches is a deeper yellow than elsewhere on the body. On the back the tubercles do not form a true mosaic pattern, as a junction zone between a light and a dark patch may run across tubercles and thus a single tubercle can be spotted with dark pigment at one end, but not at the other. The tentacles of *L. grossui* are grey and not bluish like those of *L. flavus*. The sole of the foot is straw-coloured and the small foot fringe is bordered dorsally by a pale yellow-grey area. Characteristic of the genus *Limax*, the mantle is concentrically grooved, like a thumb print with its nucleus in the centre of the shield.

These observations essentially agree with Lupu's description, although she does not mention the greenish colour. The length of the body quoted (50 mm) is that of a preserved specimen rather than a live slug (Lupu, 1970). Live adult specimens of *L. grossui* collected in Ireland measured from 70 to 95 mm in length when fully extended.

INTERNAL FEATURES

This description of the internal features of *L. grossui* relates to the dissection of an unfixed specimen, 75 mm in length, collected from deciduous woodland at Springhill, Moneymore, Co. Londonderry on 2 October 1975. However, the internal anatomy agrees with other green *Limax* from Ireland which have been dissected (Chatfield unpublished).

Fig. 1 shows a diagram of the reproductive system of *L. grossui*. The organs have been rearranged from their original position to display the system, and the penial retractor muscle has been cut to allow the penis to be positioned on the right, thus showing the details of the insertion of the spermatheca duct, oviduct and vas deferens. The grey ovotestis is situated halfway down the body amongst the yellowish-brown lobes of the digestive gland on the left hand side of the slug. It measured 9×5 mm. Leading from the ovotestis is the narrow convoluted small hermaphrodite duct which runs for about 20 mm, anteriorly and then posteriorly to join the albumen gland at its anterior end. The small hermaphrodite duct is conspicuous as it is intense white in colour. The albumen gland is a large cream coloured organ 18 mm long by 8 mm wide which lies on the ventral side of the body. A small white seminal vesicle is present at the anterior end of the albumen gland. The large hermaphrodite duct leads anteriorly from the albumen gland into the region of the head. This duct is translucent white, with some deeper white glandular tissue, and in the anterior part of the slug dissected, the prostate gland was chrome yellow, as recorded also for *L. flavus* (Quick, 1960). Although internally there are separate male and female tracts in the large hermaphrodite duct, these separate in the anterior region into a slender vas deferens of less than 1 mm width and an oviduct of 2 mm width. When the penis is in its natural position between the tentacles, the vas deferens loops round the grey sheath of the right tentacle to join the penis at its posterior end. The penial retractor muscle is also inserted at the posterior end of the penis and its other end attached to the wall of the diaphragm at the back of the mantle shield, near the chrome yellow kidney on the left hand side of the animal.

The penis is a simple c-shaped structure 18 mm long, 4–5 mm wide and whitish in colour. The spermatheca is a membranous bag, and in the specimen dissected this contained a pink deposit. The bulb measured 9×3 mm and it was attached to the penis by a thin membrane. The spermatheca duct leading from the bulb was 6 mm in length and 1 mm wide and it was attached by a membrane to the oviduct. When the membrane was

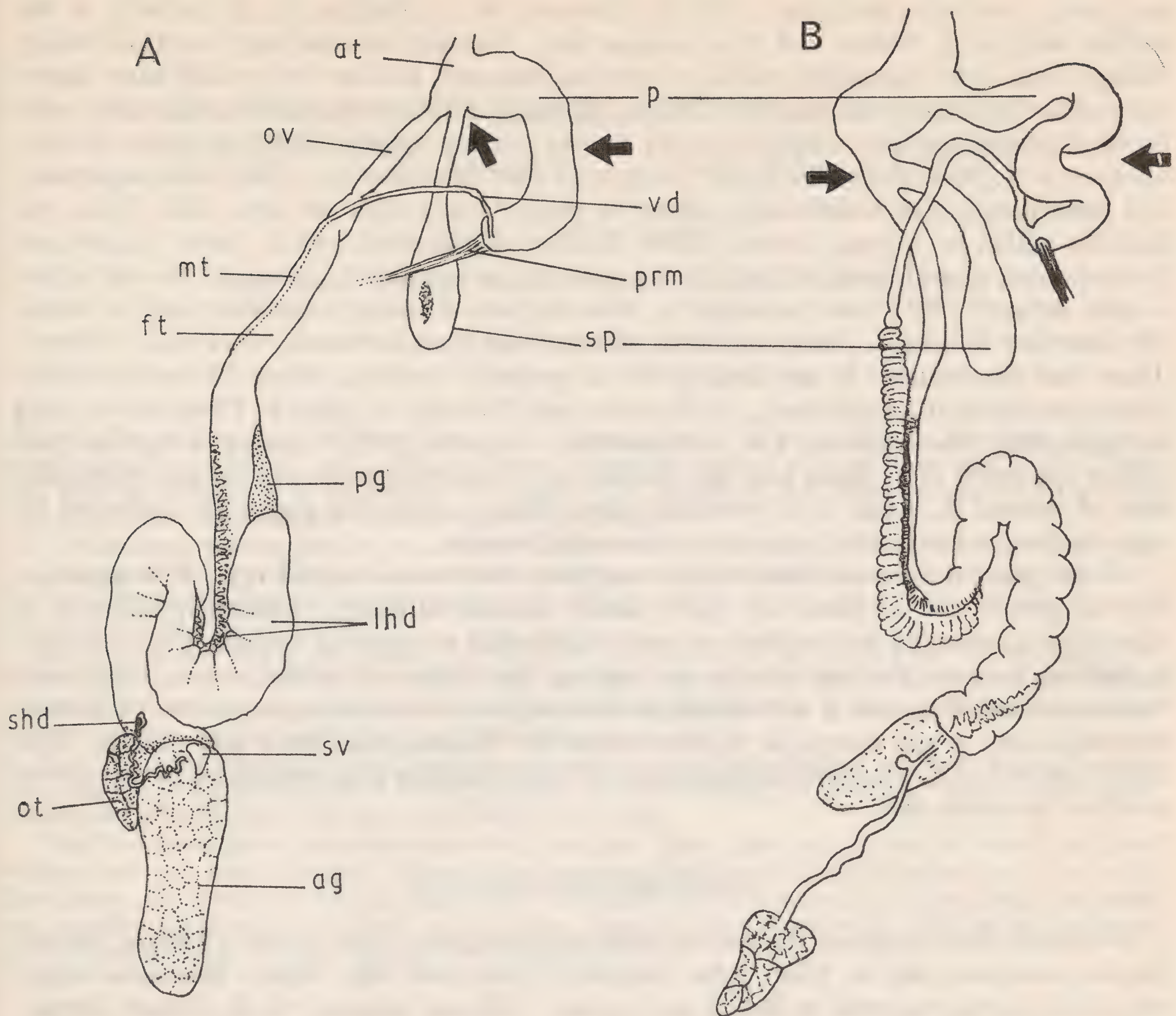


Fig. 1. Reproductive systems of *Limax grossui* Lupu (A) and *L. flavus* L. (B) to show principal differences (arrowed). ag albumen gland; at atrium; ft female tract; lhd large hermaphrodite duct; mt male tract; ot ovotestis; ov oviduct; p penis; pg prostate gland; prm penial retractor muscle; shd small hermaphrodite duct; sp spermatheca; sv seminal vesicle; vd vas deferens. B. redrawn from Quick 1960, fig. 14B, published by permission of the Trustees of the British Museum, Natural History.

dissected out, the insertion point of the spermatheca was revealed near the base of the penis.

The distinction of *L. grossui* from *L. flavus* on anatomy is based on the penis and the spermatheca. In *L. grossui* the penis is c-shaped, whereas in *L. flavus* it is more elongate and s-shaped (cf. figs. 1A and B). The spermatheca duct of *L. grossui* is inserted at the base of the penis and not on the oviduct as in *L. flavus*.

In addition to differences in the reproductive system, Lupu (1970) also distinguishes between the two species in the length of the intestinal appendix which extends almost to the tip of the tail in *L. flavus* but not in *L. grossui*. Further dissections and measurements are needed to check this in the Irish material.

DISCUSSION

The non-marine molluscan fauna of Ireland was worked extensively in the nineteenth

and early twentieth centuries by P. H. Grierson, R. A. Phillips, R. F. Scharff, A. W. Stelfox and R. J. Welch and it is curious that this slug has not been spotted before. Many of the Irish naturalists relied on external features, and so they would have missed the marked difference in anatomy. Although many nineteenth century naturalists were quick in describing new varieties in the known species, Quick (1960) records only four varieties of *L. flavus* and Stelfox (1911) reported that 'No variation of any real importance has been noted, but occasionally lighter or darker specimens are met with'. From the habitats which he quotes, it seems likely that he encountered both *L. flavus* (in gardens, green-houses, churchyards, cellars, larders and sculleries) and *L. grossui* in the old native woods. Scharff (1891) also recorded *L. flavus* in both domestic situations and in woods. He describes finding *L. flavus* under the bark of old trees in woods, always in a cluster. These last observations fit my findings for *L. grossui* in Ireland, where 19 were recorded under one stone at Lough Scur, Co. Leitrim and 25 found by Mrs. E. Platts under a log at Springhill, Moneymore, Co. Londonderry. Scharff (1891) figured a typical pale yellow specimen of *L. flavus* and his drawing of the reproductive system also resembled that of normal *L. flavus*. It is probable that, when writing his paper, he collected his animals from a convenient source in a domestic location.

From general external resemblance and from the lemon-shaped eggs, it is apparent that *L. grossui* and *L. flavus* are quite closely related, although sufficiently different in appearance, anatomy and ecology to merit distinction as separate species. The difference in habitat between the two species also reduces the chance of hybridization. Field work has shown that *L. grossui* is widespread in Ireland, but not common in the rest of Britain, although there is one record for Wales, which, like Ireland, also has a wet climate. With Lupu's record of *L. grossui* in Roumania, it is likely that this slug remains to be discovered in other countries also.

ACKNOWLEDGEMENTS

It is a pleasure to thank the various staff and associates of the Ulster Museum, Belfast, Dr. R. Anderson, Mr. R. Nash, Mrs. Elizabeth Platts and Mrs. Helena Ross who helped me collect during my visit to Belfast in October 1975 and also Mr. C. D. Deane, Deputy Director of the Ulster Museum for release of his staff to help with the field work. Dr. M. P. Kerney provided the final impetus for the writing of this paper and various members of the Conchological Society have helped in the past on collecting trips and by sending specimens. I am most grateful to Mr. A. E. Ellis for reading the manuscript.

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STUDIES ON FOOD AND FEEDING IN SOME EUROPEAN LAND MOLLUSCS

JUNE E. CHATFIELD

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(Presidential Address, delivered 22 February 1975)

Abstract: The feeding habits of some European pulmonate land slugs and snails are described. Although commonly pests in gardens, only a few species are necessarily injurious to crops. Most feed on wild plants and often on dead parts of the plants. The majority are herbivores, but others include omnivores and carnivores: many are important in the breakdown of detritus.

The feeding apparatus consists of a buccal mass housing a radula, jaw, odontophore cartilage, radula sac and a complex of muscles which operate the buccal mass during feeding. Snails feed by circular movements of the radula and jaw which together bite off pieces of food. Both show wear and old teeth are periodically shed from the radula.

Slugs and snails usually feed at night or at dawn. The position of food in the gut was determined by dissecting snails collected in the field at 4-hourly intervals. The crop was usually full early in the day but emptier later on. In spring and summer most snails dissected had fed, but in winter others had no food in the gut. Faeces were produced from 1½ to 7 hours after feeding.

Food plants in gut contents and faeces can be identified by their detailed structure. *Monacha cantiana* and *Hygromia striolata* fed mainly on *Urtica dioica* and *Anthriscus sylvestris*: *M. cartusiana* mainly on dead grass. Proportions of food plants in the gut varied with time of year.

The literature suggests that snails may select their food. Some plants are rejected on taste: hard plant surfaces may also inhibit feeding. Different plant communities support differing proportions of palatable food plants. Disturbed ground yields many, and chalk grassland fewer, proven food plants. Slugs and snails are probably important in the decay of dead plant material. Plant fragments in snail faeces are further decomposed by other animals, fungi and micro-organisms.

The animals to which I shall refer this afternoon are land snails and slugs. These molluscs belong to the class Gastropoda and to the sub-class Pulmonata. Pulmonates are typically air-breathing snails without the operculum or plate closing the mouth of the shell (seen in the common winkle) which is characteristic of the Prosobranchia, the other sub-class including some land snails. All but two of the British land Mollusca belong to the Pulmonata. Within this group are snails which have a well developed shell, and slugs with either a small vestigial shell (usually internal) or no shell at all.

SLUGS AND SNAILS AS PESTS

Most people are familiar with slugs and snails in gardens where they may do considerable damage to crops, and thus it is the larger species which are the most well-known to the layman. In spite of the economic interest in the damage to crops by slugs and snails, comparatively little detailed work has been published on the feeding habits of land molluscs. With the possible exception of the large common garden snail, *Helix aspersa* Müller, most of the damage to crops is done by slugs, of which eight to ten species are commonly found in gardens and on agricultural or horticultural land. Stephenson (1968) considers *Agriolimax reticulatus* (Müller), *Arion hortensis* Férussac and *Milax budapestensis* (Hazay) to be major pests and *Arion circumscriptus* agg., *A. intermedius* Normand

and *Milax sowerbyi* (Férussac) to be less common amongst crops. The British potato industry is one particularly affected by slugs (Runham and Hunter, 1970). *Milax budapestensis* and *Arion hortensis* often live in soil where they burrow into and feed on ripe potato tubers. It is possible that existing damage by potato wireworm larvae *Agriotes* spp. encourages slugs which detect the odour of potato when the skin is broken by wireworms. Slugs in the vicinity may then move in to feed on the already damaged potatoes. Once inside the tuber, slugs can devour most of the interior of a potato (as they did in my garden last year!) and those which are only lightly infected are unmarketable and represent a loss to the commercial grower. Slugs are also responsible for damage to winter wheat through eating the wheat germ and thus preventing germination or by destroying the small leaves of young seedlings (Runham and Hunter, 1970). The small grey field slug *Agriolimax reticulatus* often occurs in large numbers and it will feed on plants in gardens. It is the slug most commonly washed out of lettuces being prepared for the table. However, most lists of food plants of *A. reticulatus* relate to its diet in the wild (Frömming, 1954; Pallant, 1969 and 1972). Although it does eat crops in gardens, it is probable that it will also feed on many common weeds, as this trend was suggested by results of laboratory feeding experiments (Duval, 1971 and 1973). The large black or red slug, *Arion ater* agg., is particularly common in gardens where, due to its size, it can do considerable damage to garden plants. It also feeds on decaying material and is often very abundant crawling across compost heaps at night.

However, not all slugs and snails need be included under the heading of pests, for only a certain proportion of the fauna lives on cultivated ground and many are too small to do the sort of damage which we normally associate with slugs and snails. The majority of land molluscs in Britain feed harmlessly on wild plants and it is very often the dead parts of the plant which they eat.

THE VARYING DIETS OF SLUGS AND SNAILS

Land snails and slugs have exploited a range of feeding opportunities in their natural habitats, but the majority of them feed on plants rather than animals. Most slugs and snails are herbivores, eating either fresh or senescent plant material: the larger species of pulmonates feed on flowering plants which make up the bulk of the living vegetation in the environment. Slugs and snails, like other animals, rarely feed on mosses and liverworts although occasional moss leaves are sometimes reported in faeces (Grime and Blythe, 1969 and Pallant, 1969). In contrast, many of them will feed on the larger fungi and lichens. In woodland during autumn, it is a common sight to see toadstools, like *Russula*, with large pieces of the coloured cap eaten away by slugs, and in moist weather one is often able to observe a slug actually feeding on the fungus. Peake and James (1967) reviewed the references to non-marine molluscs feeding on lichens and they gave a wide range of examples with snails from eight families and slugs from two families known to eat lichens. Although the smaller species feed on fine lichen crusts, some of the larger snails will consume both macro- and microlichens. Snails will also browse on the green film of unicellular algae growing on tree trunks and some rock surfaces. *Discus rotundatus* (Müller) has been recorded feeding and growing on a diet of green algae present on pieces of chalk in both laboratory and field situations (Barrett and Chatfield, 1973).

Some molluscs are not confined to food of plant origin and may eat both animal and plant material. These are the omnivores and a classic example is the glass snail, *Oxychilus*. Taylor (1907) reports that *O. cellarius* (Müller) will eat small worms, eggs of *Arion ater* agg. and other molluscs in addition to cryptogamic vegetation (lichens, mosses etc.). More recently Rigby (1963) examined the faeces of *Oxychilus* and reported that green material was rarely found in the gut, and that the faeces contained much decaying plant

material: this was probably derived from leaf litter and decaying wood. Studying woodland snails at Whytham Wood, Oxfordshire, Mason (1970) showed that the faeces of *O. cellarius* and *O. alliarius* (Miller) contained significantly greater amounts of animal material than those of other species of snail living in the same habitat.

Another example of an omnivorous feeder is the large black or red slug *Arion ater* agg. which is often to be seen after rain feeding on other slugs that have been squashed on a footpath or roadway (Boycott, 1934). A demonstration of the carnivorous opportunism of this slug was seen recently in the museum. A batch of assorted slugs was placed in a solution of the narcotic MS222 in preparation for freeze-drying (a comparatively new technique used in the preservation and display of specimens in museums). Some of the slugs were more sensitive to the narcotic than others and quickly relaxed. One large *A. ater* agg. proved remarkably resistant and after devouring some of the smaller slugs, it was caught in the process of eating a large narcotized *Limax flavus* L., and it had already eaten the anterior half before its activities were discovered!

Dead animal material, including earthworm chaetae and arthropod fragments, is often recorded from the faeces of land molluscs (Pallant, 1969, 1972 and Mason, 1970), but in most species these only account for a small percentage of the total faecal material. It is possible that many of these may be taken in accidentally as the snail browses at ground level.

The three species of *Testacella* in Britain are examples of true carnivores. They are subterranean and live on a specialized diet of soil animals including earthworms, slugs and centipedes. On account of the burrowing habits, the shelled slug, *Testacella*, (which has an external shell plate near the tail) is only found sporadically and usually in gardens. Runham and Hunter (1970) give a graphic account of the way in which *Testacella* tackles an earthworm using the needle-like radular teeth.

Whilst some of the land molluscs feed on living material, many eat dead and often decaying food. This is probably true for many of the small species of snails which are commonly found in leaf litter. Observations have shown that decaying plants often have fungal hyphae growing on them, but how much nutriment snails obtain from micro-organisms like bacteria, protozoa or fungal threads amongst their food is not known.

Another way of dividing the feeding habits of molluscs into categories is by the size of the food particle. Molluscs which feed on large pieces of food (on land the flowering plants and larger fungi) are described as *macrophagous* whereas those feeding on small particles (bacteria, algae, fungal threads, and powdery lichens) are described as *microphagous*. It is possible for the same species of land snail to take opportunity of both types of feeding. Graham (1955) suggests that the microphagous diet is the primitive one for the Mollusca as a whole and is connected with the need for particles of food small enough to be ingested by individual cells of the digestive gland since part of the digestive processes of molluscs takes place inside the cell. Macrophagous molluscs rely to some extent on further mechanical breakdown of their food or on a large intake with a high wastage. The large number of identifiable plant fragments in the faeces of land snails illustrated (Plates 1 and 2) is an example of the wastage involved.

THE FEEDING PROCESS

The adaptation of the buccal mass (or mouthparts) to feeding is well demonstrated by the efficiency and speed with which pest species can damage a crop. The following observations on the structure of the mouthparts and the way in which they function in feeding were made on the land snails *Monacha cantiana* (Montagu) and *M. cartusiana* (Müller), but a similar structure and functioning occurs in many of the herbivorous land molluscs. The feeding apparatus of slugs and snails, like that of most gastropods, is a

complex structure, especially when studied in detail. The buccal mass is a large white muscular organ leading from the mouth and situated in the anterior part of the head between the sheaths of the two large tentacles. It is easily seen on dissection. The buccal mass comprises the buccal cavity, the radula (a tongue-like structure with many teeth) supported by the odontophore, the radula sac (a small protrusion in which new radular tissue is continuously secreted), the odontophore cartilage, the jaw and a complex series of muscles which operate the buccal mass. The structure of the buccal mass has been described in detail for the land snail *Helix aspersa* (Crampton, 1973). Illustrations of the general anatomy of the alimentary canal of a land snail *Helix* are to be found in a number of zoology textbooks (e.g. Rowett, 1961).

Some of the movements of the buccal mass during feeding can be observed in a living snail. A good method for observation is to allow a snail to crawl on a sheet of glass or perspex. The feeding movements of the animal can be observed both in side view and ventrally, when viewed through the glass. Using large species like *Helix aspersa*, it is easy to see the jaw (which is brown in colour) and the radula (colourless), however very young specimens or the smaller species, (e.g. *Monacha cantiana*) are best to observe the movement of the buccal mass which can be seen moving within the snail when the body wall is relatively unpigmented. Hungry snails (starved before observation) can be induced to feed by using a plate of glass on which a thin veneer of flour and water paste has been allowed to dry.

Observations on *Monacha cantiana* and *M. cartusiana* showed that well-fed snails would crawl but did not give feeding movements. In these the outer lips were extended ventrally in front of the mouth (Fig. 1a). Starved snails would feed immediately: the outer lips separated revealing the upper or oral lips (Fig. 1b). The median cleft in the lower oral lip became obliterated as the mouth opened, allowing a wide gape through which the radula protruded. The jaw was then visible near the dorsal wall of the mouth and the radula scraped against it, breaking off pieces of food which were subsequently released into the buccal cavity and swallowed.

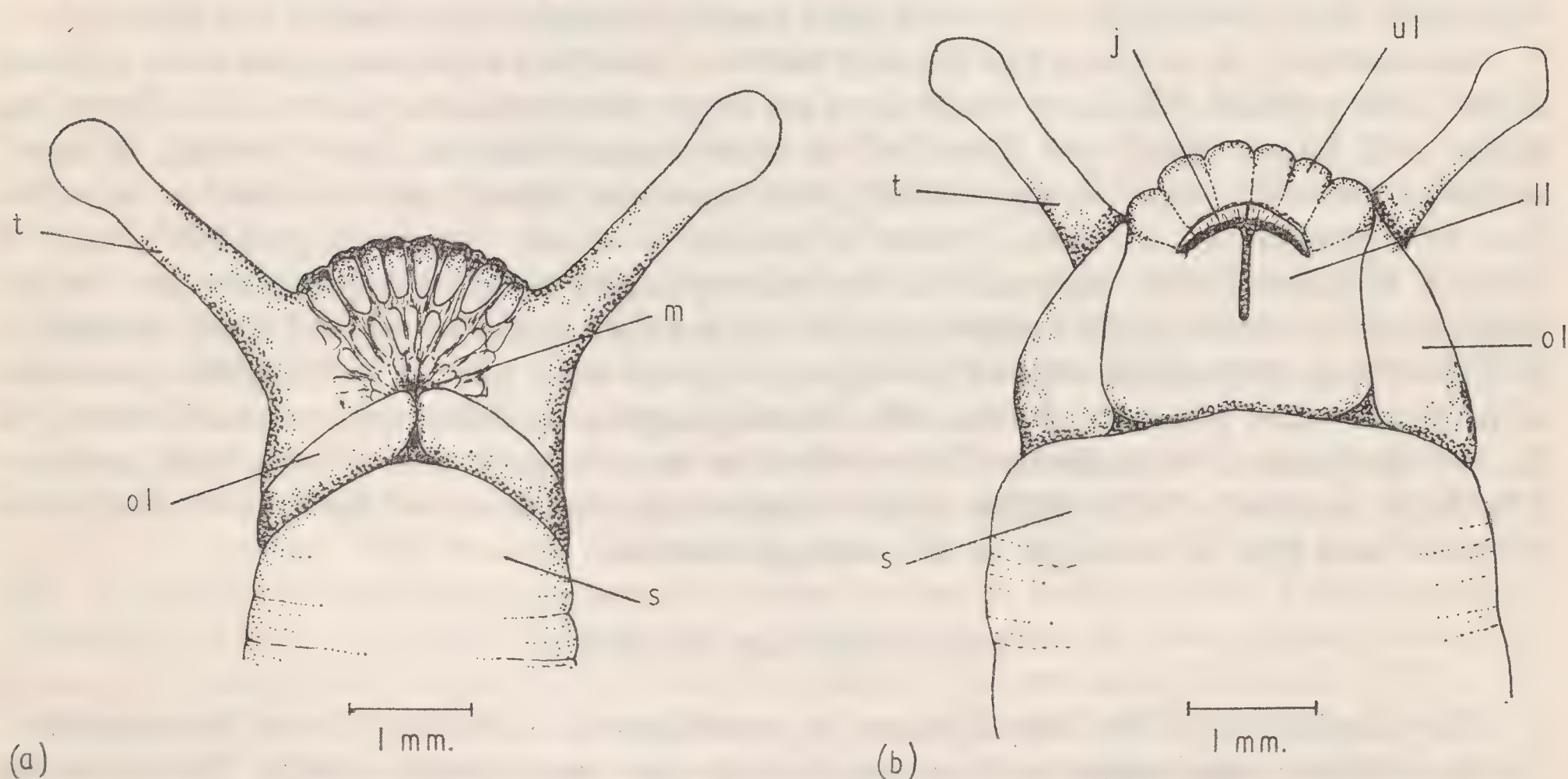


Fig. 1. The mouth and anterior part of the foot of a snail viewed ventrally through a glass sheet. (a) *Monacha cartusiana* (from the Camargue, France) showing the mouth closed and the outer lips together; (b) *M. cantiana* (from Southridge, Berkshire) in a feeding position showing the outer lips separated and the jaw protruding. j jaw; ll lower lip; m mouth; ol outer lip; s foot sole; t anterior tentacle; ul upper lip.

Viewed from the side, the cycle of movement of the buccal mass showed the odontophore (with radula) moving anteriorly and then dorsally. At the same time the jaw moved anteriorly and then ventrally. The radula then rotated slightly and moved posteriorly scraping against the biting plate of the jaw. A section through the head of a slug showing the relative position of the structures involved is figured in Runham and Hunter (1970). Food like a crisp lettuce leaf will crunch and break as the radula and jaw meet: it is possible to hear this. Less turgid food is pulled into the mouth by the posterior and ventral retraction of the odontophore. Before the feeding cycle starts again, the radula and jaw separate, the jaw moving posteriorly and dorsally and the odontophore (carrying the radula) posteriorly and ventrally.

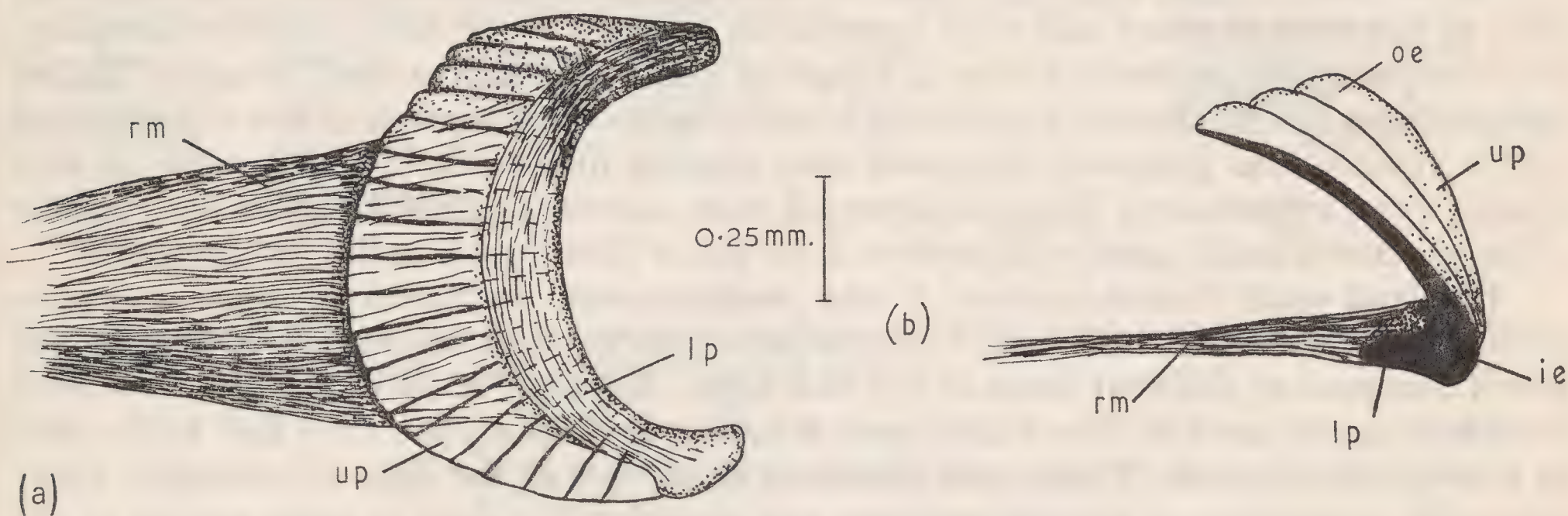


Fig. 2. The jaw of *Monacha cantiana* (from Play Hatch, Berkshire) to show the upper and lower plates and the attachment of a retractor muscle. (a) dorsal view; (b) lateral view shown as a section through the jaw. ie inner edge; lp lower plate; oe outer edge; rm retractor muscle; up upper plate.

Fig. 2a-b shows the structure of the jaw of *M. cantiana* in surface view and in section. The chitin is at its thickest at the biting plate (inner edge) of the jaw which scrapes against the radula. Both radula and jaw of slugs and snails are subjected to wear as a result of constant use and, sometimes, the abrasive properties of their food. Scanning electron microscope studies on the jaw of the slug *Agriolimax reticulatus* have demonstrated marks at the edge caused by the teeth on the radula (Runham and Hunter, 1970) and there are also pictures published showing wear on individual radular teeth of some land snails (Solem, 1974). Old worn radular teeth of the anterior (front) row become detached and are often swallowed with the food. It is not unusual to see small chains of detached radular teeth in the gut contents of a slug or snail. New tissue is continually secreted in the radula sac and the next row of teeth takes the place of those detached. The anterior toothed area as a whole is probably involved in feeding and the front row of teeth is not the only functional row of teeth. From one to five new rows of teeth are known to be produced per day for slugs and it is also known that environmental factors like temperature affect the rate of production of new teeth (Runham and Hunter, 1970). Typical of herbivorous land molluscs, most British slugs and snails have a radula with many teeth in each row and many rows of teeth in different stages of development. Individual teeth of the radula have cusps or projections and there is a wide variation in the shape of teeth in pulmonate land snails. Similar to the human situation, the teeth at the side of the mouth are usually a different shape from those in the centre. The recent use of the scanning electron microscope has done much to increase our knowledge on the shape and detail of molluscan radulae as it produces photographs with an exceptionally good depth of focus. Many such striking illustrations are shown in Solem's book (1974).

Slugs and snails are primarily nocturnal animals which crawl and feed after dark, although they are sometimes seen crawling in the daytime during damp weather. Diurnal rhythms have been studied in the slug *Agriolimax reticulatus* using time-lapse cine-photography (Newell, 1966). The results of this demonstrated the essential nocturnal pattern of activity and the sequence of different types of behaviour such as feeding, crawling, resting and mating.

Cameron (1970) studied the daily pattern of activity of three helicid snails *Cepaea nemoralis* (L.), *C. hortensis* (Müller) and *Arianta arbustorum* (L.) by observation, recording their activity each hour for 24 hours in a laboratory situation. The snails were exposed to sixteen hours of light and eight hours of darkness (which matched the situation in the field at the time of year) and they were in an atmosphere of 100% relative humidity. Experiments were performed over a range of constant temperatures: those at higher temperatures (26°C) showed a high level of nocturnal activity whereas at low temperatures (0°C) activity was generally depressed and showed little variation with time of day. During these experiments Cameron detected some interesting differences in the response of the species of snails used, with *Arianta* more active than *Cepaea* at low temperatures.

The land snail *Monacha cantiana* is also predominantly nocturnal. A series of experiments was undertaken to investigate the relative position and abundance of food in the gut of this snail at different times of day and night. A sample of snails was collected from a roadside nettle patch at Play Hatch, near Reading, Berkshire (Nat. Grid Ref. 41/741762) at four-hourly intervals. These were preserved in alcohol at the time of collecting. Later the snails were dissected and the presence and abundance of food in three regions of the gut (crop, intestine and rectum) were recorded. Results are shown in Fig. 3. There was some food in the gut of most snails examined from samples taken in March, May, June and August 1966 and in April and July 1967, but a greater volume of food (shown as a large box) was present during the morning in samples taken from 02.00–11.00 hours G.M.T., and much of this food was still in the crop (shown black). By the early evening, although the intestine and rectum of the dissected snails were still well packed with food, the crops of about half of the snails were empty. The time at which food was ingested varied according to the time of year and to local weather conditions. The results for June 1966 and July 1967 showed little food present in the crops of the snails collected in late evening between 22.00 and 23.00 hours G.M.T. During the height of summer, when the evenings are light, *M. cantiana* did not usually become active and feed until late in the evening at dusk. However in the samples taken at other times of year, notably April 1967, May 1966 and August 1966, most of the snails had started to fill the crop by 22.00–23.00 hours. The particularly early activity of the snails in August 1966 was probably due to the wet weather and overcast conditions during that afternoon. In summary, these experiments showed that feeding was a daily activity and each snail would normally fill its gut with food during the course of the night. During the daytime the food would pass through the gut, with waste expelled as a faecal string from time to time. However all the observations shown in Fig. 3 were made during spring and summer when snails are usually active. Some examples of *M. cantiana* were taken during the winter months and on dissection these showed no food in the gut when temperatures approached freezing. Under these conditions *M. cantiana* is often inactive at ground level with an epiphragm sealing the mouth of the shell (Chatfield, 1968).

The rates at which food passed through the alimentary canal of snails were tested in some laboratory experiments which were set up using snails that had been starved for a few days prior to use. These snails were fed on different types of food which was available in excess under humid conditions. The snails were kept under observation, and records

made of the time at which each snail fed and that of the eventual expulsion of a faecal string. Experiments were set up using *M. cantiana*, *M. cartusiana* and *Hygromia striolata* (Pfeiffer) and the results are shown in Table 1.

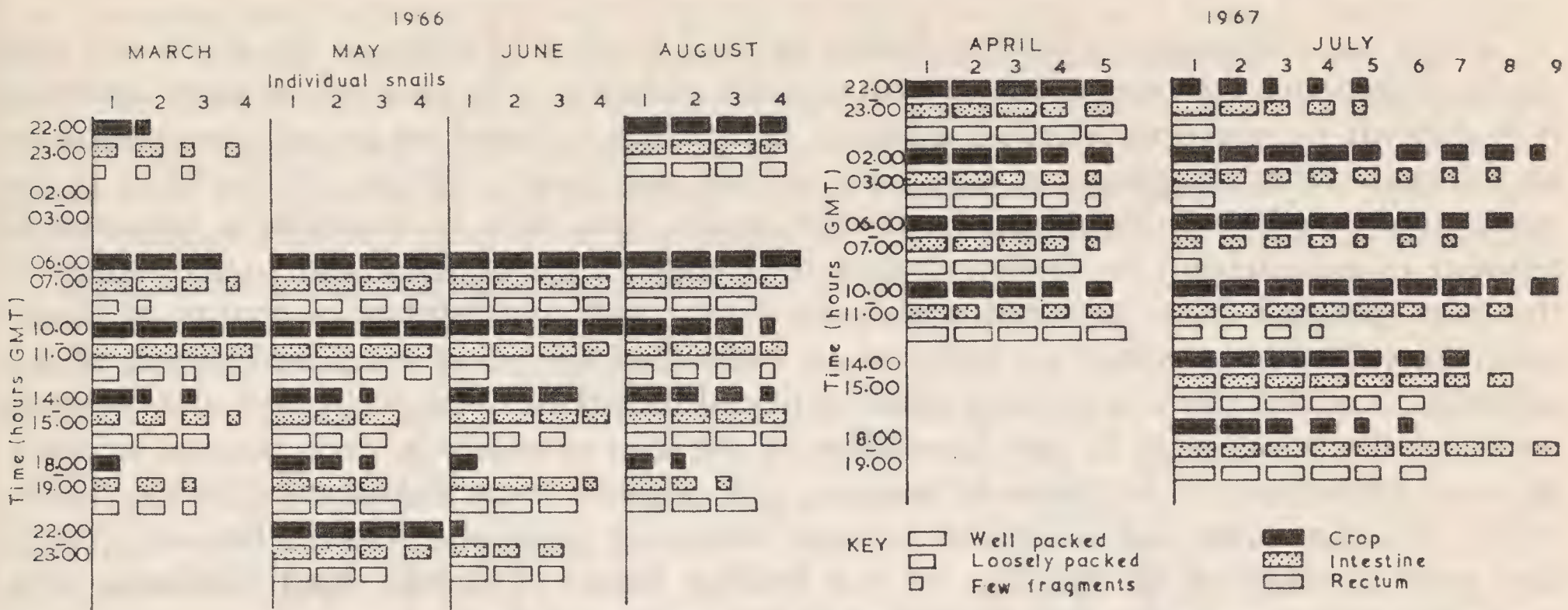


Fig. 3. The distribution and volume of food present in the gut of *Monacha cantiana* collected from Play Hatch, Berkshire, at regular intervals of time, through day and night.

TABLE 1. Time taken for the passage of food through the gut of some European land snails

SPECIES	TIME	FOOD MATERIALS					
		Lettuce	<i>Armoracia</i>	<i>Urtica</i>	<i>Urtica</i>	Dead stem	Rolled oats
		Hr./Min.	<i>rusticana</i> leaf	<i>dioica</i> leaf	<i>dioica</i> stem	Hr./Min.	Hr./Min.
<i>Monacha cantiana</i>		5.13					8.30 11.35
<i>M. cantiana</i>		3.26					4.45
(from Italy)		6.10					
<i>M. cartusiana</i>		2.45	1.55	2.00	1.55	1.20	2.40
(from France)		3.10	1.33	3.55		2.05	2.10
		3.50	2.00	3.00		2.30	2.00
		3.35	1.25				
			2.20				
<i>Hygromia striolata</i>		7.40	7.15				11.45 8.30

Identical foods took different times to pass through the gut of different species of snail. *Monacha cartusiana* passed lettuce through the gut in 3 hours, compared with 5–6 hours for *M. cantiana* and 7 hours for *Hygromia striolata*. A range of foods was used with *Monacha cartusiana* and these passed through the gut at different rates. Horse radish leaves (*Armoracia rusticana* Gaertn., May & Scherb), stem of cow parsley (*Anthriscus sylvestris* (L.) Hoffm.) and stinging nettle stem (*Urtica dioica* L.) were eaten and passed through the gut in 1½–2½ hours, whereas stinging nettle leaves took 2–3 hours and lettuce 3–4 hours to pass through.

However the faeces produced in these experiments represented only part of the initial intake of food, for whilst some of the food passes through the gut in a matter of hours, other particles from it are taken up into the digestive gland and retained for several days where some of the digestion takes place, principally inside the cells of the gland (Walker,

1972). Waste material ejected from these cells is passed back into the stomach and forms a dark brown strip of fine particles along the faecal string. This is known as the liver string.

FEEDING IN THE NATURAL HABITAT

There are references to feeding habits of land snails and slugs in the literature and many of them are the work of nineteenth century naturalists. In some of the early accounts it is difficult to interpret whether a report on feeding is based on actual observation or an inference from the plant on which the animal was found. Taylor (1894–1921), in his monograph on British land and freshwater snails, was able to assemble a remarkable amount of information on feeding habits of a wide range of slugs and snails. Much of this was gleaned from personal communications and unpublished accounts of many naturalists. However, when an entry of an individual species is examined, much of the information given refers to feeding under artificial situations in captivity and one becomes aware of the many gaps in our knowledge of the diet of snails in their natural habitat. In some situations, as for *Monacha cantiana*, gut contents were examined (Taylor, 1894–1921), but they were not identified beyond 'decaying grass and leaves'. Boycott (1934) also gave a range of information on the feeding habits of British land Mollusca with particular reference to the role of feeding in the ecology of snails.

More recently malacologists have reviewed and investigated feeding in a variety of European land snails and slugs. In his two books, Frömming (1954 and 1962) gives a wide coverage of information including many illustrations of plants damaged by slugs and snails and a considerable amount of data relating to feeding. However he frequently emphasizes the limits of our knowledge on this subject. In Britain a number of papers have been published in recent years describing various aspects of feeding in slugs and snails but on a limited range of species. Most of those on snails concentrate on the large helicids like *Cepaea nemoralis* (Grime, MacPherson-Stewart and Dearman, 1968; Grime and Blythe, 1969; Grime, Blythe and Thornton, 1970; Richardson, 1975; Wolda, Zweep and Schuitema, 1971 and Williamson, 1975) and *Arianta arbustorum* (Grime and Blythe, 1969), although Mason (1970) has studied feeding habits of small snails living in leaf litter. Recent papers on the natural diet of slugs are similarly restricted in species coverage and most information relates to *Agriolimax reticulatus* (Pallant, 1969, 1972).

My investigation concerned three helcid snails *Monacha cantiana*, *M. cartusiana* and *Hygromia striolata*. Existing reports on the diet of all these snails were limited. The most extensive investigation in respect of both food plants and the different species of snails studied was that of Gain, 1891, but this was based on experiments in captivity rather than the natural situation. Reports for *Monacha cantiana* included dead and living grass and leaves (Taylor, 1894–1921), *Equisetum arvense* L. (Benson, 1952), clover (van Benthem Jutting, 1933) and rotting plant material (Frömming, 1954). As food plants for *Monacha cartusiana*, Frömming (1954) lists rotting grass permeated with fungal hyphae and names two food plants, the grass *Festuca arundinacea* Schreb. and plantain *Plantago media* L. For *Hygromia striolata* Taylor (1894–1921) lists 'Arabis albida, violet leaves, primroses, petals of cultivated poppies' and Frömming (1954) reports that *Urtica dioica* is a popular food amongst *Cirsium arvense* (L.) Scop., *C. oleraceum* (L.) (thistles), *Angelica sylvestris* L. (= *Anthriscus sylvestris*) (cow parsley) and *Senecio fluviatilis* Wallr. (ragwort). Graham (1955) gives reference to *Hygromia striolata* feeding on crop plants and Step (1901) claims that it is partial to strawberries which may explain its common name 'strawberry snail'.

My investigations on *Monacha cantiana* and *Hygromia striolata* were done in south-east England (with one exception near Dieppe in France) and most samples were taken in the Reading area, Berkshire. Many of the sites were roadside habitats often with a good growth of stinging nettles. *H. striolata* was also studied at one woodland site at Norbury

Park, Surrey. The feeding of *Monacha cartusiana* in the natural habitat was investigated in France, mostly in the Dordogne and the area around Poitiers. Field work took place from 1966 to 1969.

A list of food plants eaten by the snails was established by the examination of gut contents and faecal strings taken at different times of the year and from a range of sites. The gut contents and faeces were preserved in alcohol and temporary mounts were made in Berlese fluid (which clears the tissue) for examination under a microscope. Comparing the detailed structure of the gut contents with standard mounts of identified plants from the habitat, it was possible to identify many of the fragments of food eaten by the snails. Illustrations of these are shown in Plates 1 and 2. The main features used for identification were the structure and shape of the plant hairs (trichomes), the patterns

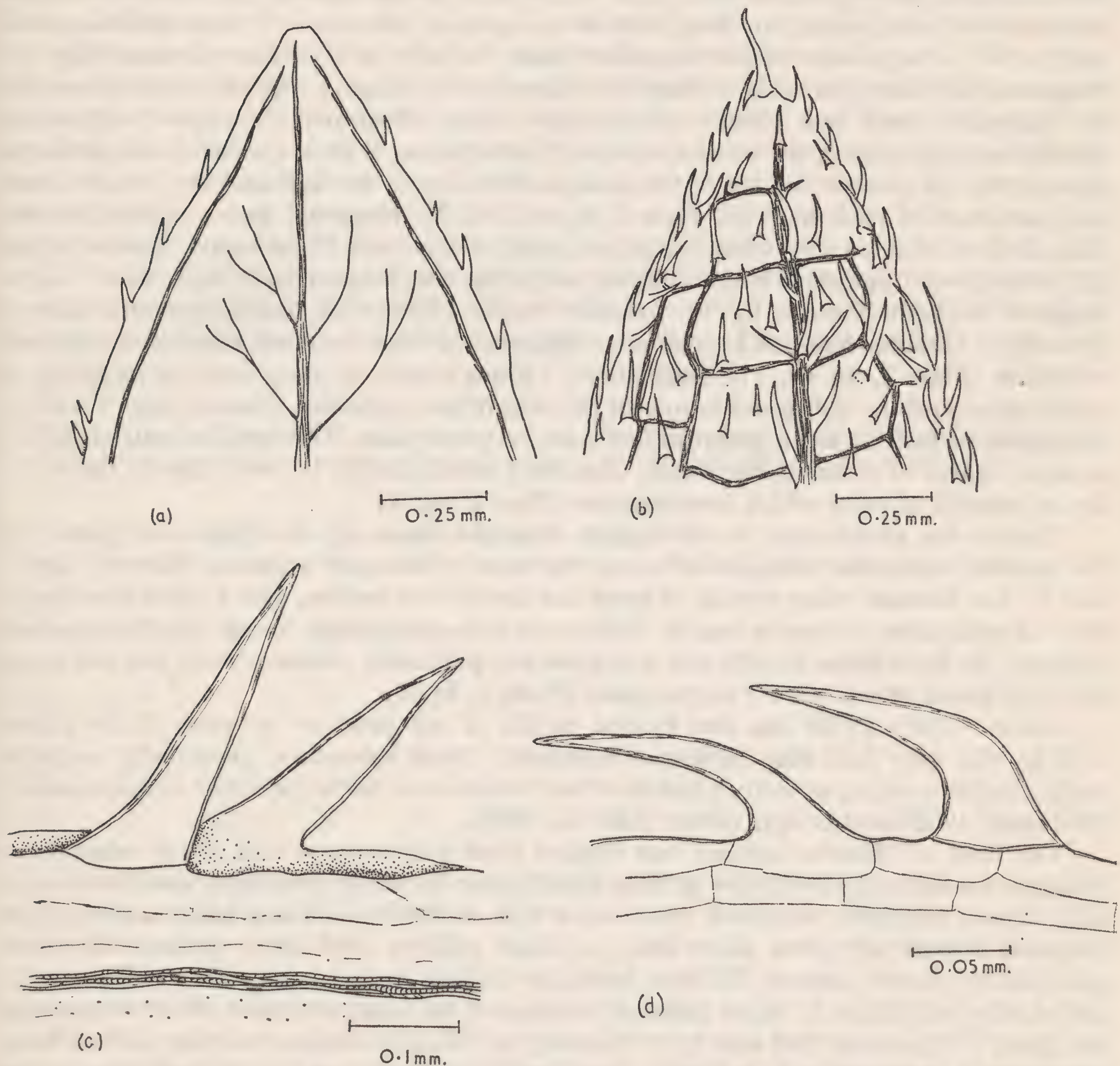


Fig. 4. Two food plants of *Monacha cantiana* to show features used in the identification of plant fragments in snail faeces. (a) leaf apex of *Anthriscus sylvestris* (cow parsley); (b) leaf apex of *Urtica dioica* (stinging nettle); (c) edge of the leaf of *Anthriscus* to show plant hairs and peripheral vein; (d) edge of the leaf of *Urtica* to show plant hairs.

of the veins (vascular tissue), the type and arrangement of stomata (which are small pores on the surface of leaves and green stems), the shape and arrangement of the epidermal cells and the presence of cluster crystals or druses. Apical fragments of some of the leaves of common wayside herbs like cow parsley were often present and these large pieces were easy to identify. Additional to the standard mounts, reference was made to several books describing and illustrating the detailed cell structure of named species of plants (Korsmo, 1954; Metcalfe, 1960 and Metcalfe and Chalk, 1950).

Fig. 4 shows the differences between leaf apices of cow parsley and stinging nettle, two very common herbs often used as food plants by *Monacha cantiana* and *Hygromia striolata*. The main difference lies in the arrangement of the veins: veins branch off from the midrib at right angles in the stinging nettle, *Urtica dioica*, and at an acute angle in cow parsley, *Anthriscus sylvestris*. In *A. sylvestris*, like other Umbelliferae, there is a distinct vein following the edge of the leaf. Most of the hairs at the edges of the leaves are simple structures in both plants, but they differ in the greater curvature of those of *Urtica dioica* and in the arrangement of the peripheral hairs in pairs in *Anthriscus sylvestris* (Fig. 4). Fragments of these plants, including the characteristic stinging hair of *Urtica dioica* with its 'ball-point' end and cluster crystals are further illustrated in plate 1. *Heracleum sphondylium* or hogweed, the other species of Umbelliferae, is distinguished from *Anthriscus sylvestris* by the greater density of the hairs at the edge of the leaf and the broader base and curvature of each hair (cf. Plate 1, figs. 1 and 2). Hogweed leaves do look hairier than those of cow parsley when examined with a hand lens. Dead nettle, *Lamium album* L., is easily distinguished from stinging nettle by the 2-segmented hairs with a slight bulge at the joint (Plate 1, fig. 8). Another common herb with multi-segmented hairs is ground ivy, *Glechoma hederacea* L., and some segments of these are often found in a collapsed condition (Plate 2, fig. 6). The field thistle, *Cirsium arvense*, is recognized by its spines of tough tissue and the polygonal nature of the cells of the epidermis (Plate 2, figs. 4 and 5). *Mercurialis perennis* L. has a glabrous leaf with very few hairs. The detailed pattern of the veins on leaves of common deciduous trees vary considerably. In beech leaves there is a dense network of veins which form squares (Plate 2, fig. 2).

Grasses are always easy to distinguish from the leaves of dicotyledonous plants by the parallel veins, the elongate cells and the rows of elongate stomata (Plate 2, figs. 7 and 8), but because many species of grass can live in one habitat, like a chalk downland, their identification to species can be difficult or time-consuming. Some, like *Brachypodium pinnatum*, do form dense swards and this grass has particular characteristics like the wavy cell wall which makes it easy to recognize (Plate 2, fig. 9).

Pallant (1969, 1972) has also figured details of cell structure of some of the plants used by the grey field slug *Agriolimax reticulatus*. Other references, potentially useful to malacologists working on feeding habits of land snails occur in the literature in mammalogy (Williams, 1962) and in agriculture (Martin, 1964).

The food of *Monacha cantiana* was studied from gut contents and faeces taken from snails on roadside nettle patches at Play Hatch, near Reading, Berkshire, and Southridge near Upper Basildon, Berkshire (Nat. Grid Ref. 41/583784). These plant communities consisted largely of *Urtica dioica* and *Anthriscus sylvestris* with some grasses, *Heracleum sphondylium*, *Cirsium arvense*, *Glechoma hederacea*, *Galium aparine* L., *Convolvulus arvensis* L. and *Achillea millefolium* L. More detailed accounts of the vegetation and site at Southridge are given in Chatfield 1968 and 1972. Feeding of *Monacha cantiana* was also studied from a grass field at Play Hatch, a *Brachypodium* dominated sward on a chalkland slope at the Ridgeway near Streatley, Berkshire (41/563813) and from a roadside bank of various grasses and herbs including *Anthriscus sylvestris* at St. Vaast near Dieppe, France in May 1967. Samples of *Monacha cartusiana* were collected in May 1967 from roadside banks at Pouzioux near Poitiers, France and Nogent near Condé, France and from a grassy field

on limestone at Thenon, Dordogne, France. Specimens of *Hygromia striolata* were collected from roadsides at Play Hatch, Berkshire (amongst stinging nettles) and near Juniper Hall, Dorking, Surrey (51/177529) and from a deciduous wood at Norbury Park, Mickleham, Surrey (51/163524). A list of food plants for *H. striolata* and *Monacha cantiana* has been published (Chatfield, 1973) and a table prepared summarizing all the reports on feeding in the three species of helicid snails studied (Chatfield, 1975).

The three species of helicid snails were shown to feed on the plants which were common in their habitats: these habitats were often disturbed roadside sites and many of the plants growing in this type of place, particularly stinging nettles, are known to be acceptable to snails. There was considerable overlap in the feeding of *M. cantiana* and *Hygromia striolata* when they were living together in the same nettle bank at Play Hatch. *Urtica dioica* and *Anthriscus sylvestris* were important food plants of both of these snails at Play Hatch and of *Monacha cantiana* at Southridge. On the roadside bank at St. Vaast, France, stinging nettles were fewer but *M. cantiana* was feeding on the abundant leaves of *Anthriscus* and some flower petals and anthers (the plants were in flower in May) were also recorded in the gut contents. In grassland situations *Monacha cantiana* fed on grass (often decayed) and on the herbs in the sward (*Lamium album* and *Glechoma hederacea* at the Play Hatch field). *Monacha cantiana* did not occur in woodland, but *Hygromia striolata* was found in woodland situations in addition to open roadside habitats. In the wood at Norbury Park and in the proximity of trees and shade near Juniper Hall, *H. striolata* had fed on the woodland herb, dogs mercury, *Mercurialis perennis* L. (Norbury Park) and on beech leaves (both sites). *Monacha cantiana* was mostly collected from grassy situations and thus rotting grass and fungal hyphae predominated in the gut contents, although at Nogent, where dicotyledon plants were available, some *Heracleum sphondylium* was recorded in the gut.

TABLE 2. Results of analyses of gut contents of *Monacha cantiana* collected at Play Hatch, Berkshire. The numbers show the percentages of the snails in each month which had fed on a particular food.

Date	No. of snails	FOOD MATERIAL									
		<i>Urtica dioica</i>	<i>Lamium album</i>	<i>Anthr. sylv.</i>	<i>Heracl. sphondyl.</i>	<i>Cirisum arvense</i>	Grass	Fungi	Seeds	Xylem	Stem
March 1966	14	50	14	71	0	0	21	35	0	71	78
May 1966	18	66	55	50	5	0	33	10	33	90	83
June 1966	25	96	32	72	28	8	24	68	16	84	76
August 1966	16	88	56	25	6	0	50	80	18	94	81

Table 2 shows differences in the proportions of food materials scored in gut contents of *Monacha cantiana* from snails taken in different months of the year (March–August 1966) from the roadside nettle bank at Play Hatch. Variations in the percentages of the food plants represented in gut contents were associated with the seasonal development of the plant community. The percentages shown in the table represent the snails out of the total sample which had fed on a certain plant, but as one individual usually feeds on more than one type of plant during the course of a night, the percentages add to more than 100. From these results, several points emerged. *Urtica dioica* and *Anthriscus sylvestris* were the two most abundant food plants eaten and constituted the major part of the diet of *Monacha cantiana* at that time of year. Feeding on *Urtica dioica* showed a steady increase with 50% of the snails feeding on this plant in March and about 90% in June

to August when the nettles were up to 100 cms high. Some of the March records were of dead stems and leaves of *U. dioica* which were probably eaten by snails feeding at ground level. *Anthriscus* was an important food during the spring as leaves of this plant were well developed from January onwards with the plants growing steadily until flowering in May. After seeding, the flowering shoots of *Anthriscus* died off in July, and in August many of the pieces of cow parsley recorded in gut contents were of recently dead stems or leaves. There was a secondary growth of leaves of *A. sylvestris* resulting from bank mowing at Play Hatch which took place in June.

Lamium album, although not a major food plant, was found in gut contents. It was persistently present in the habitat at Play Hatch throughout the year. *Heracleum sphondylium* was not uniformly distributed on the bank, but on account of the large size of its leaves which matured in June and July, it was found in 28% of the gut contents of *M. cantiana* during June 1966. *Cirsium arvense* was not particularly abundant in the Play Hatch nettle bank and correspondingly it was represented in only 8% of the samples in June.

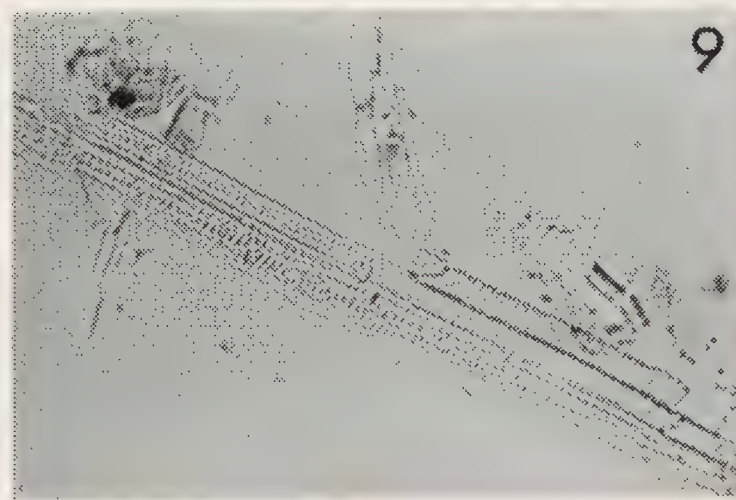
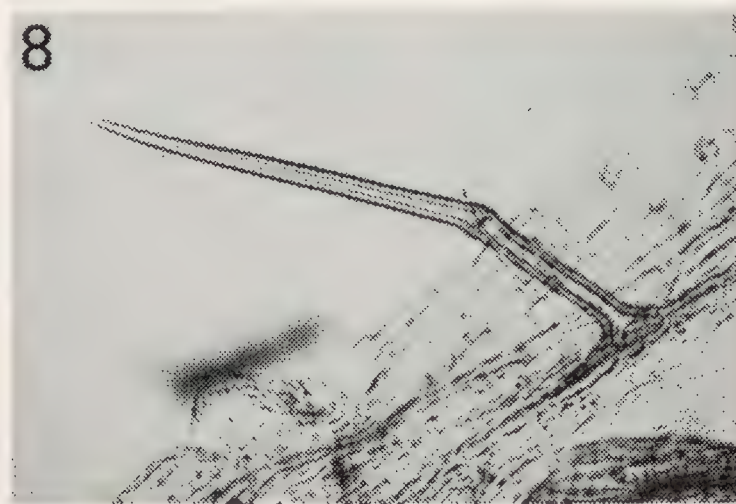
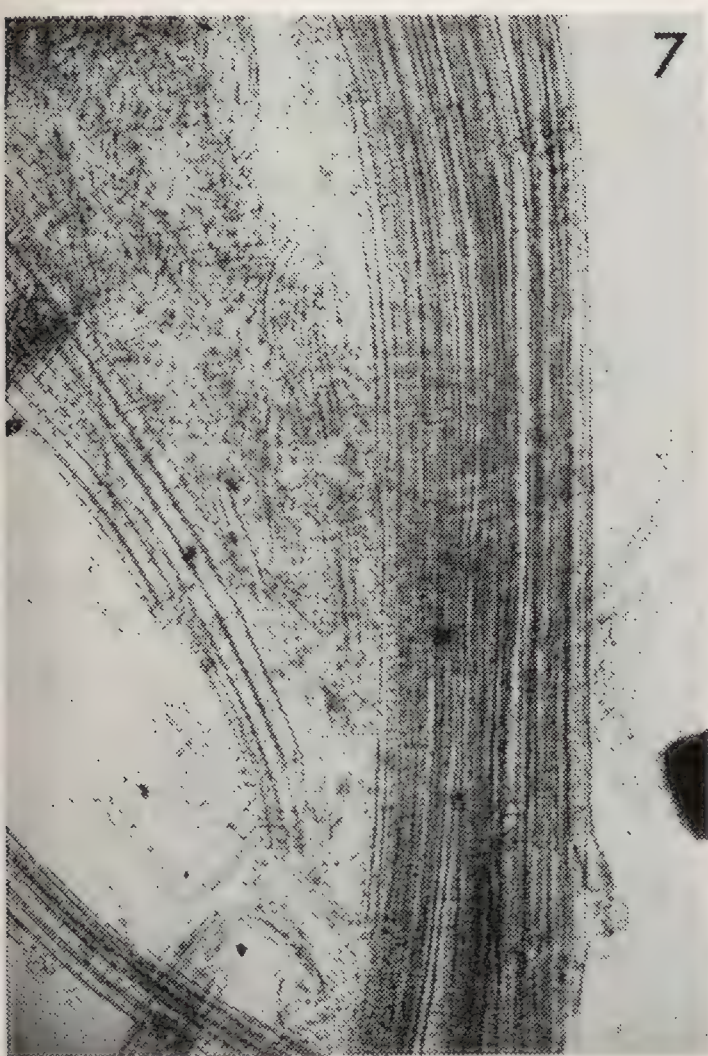
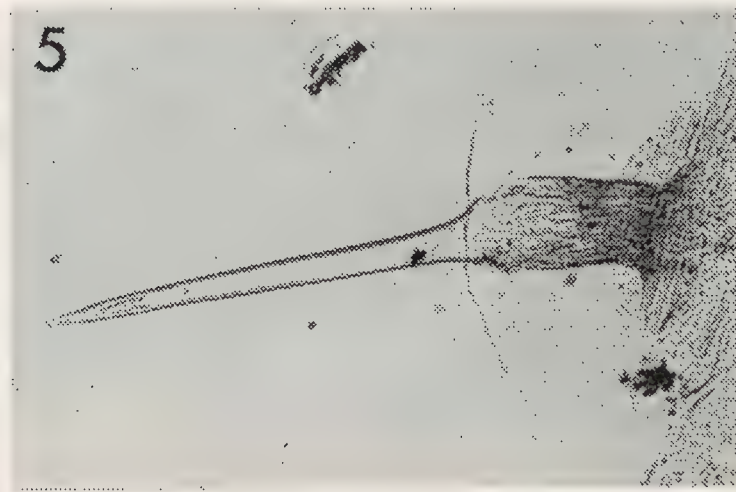
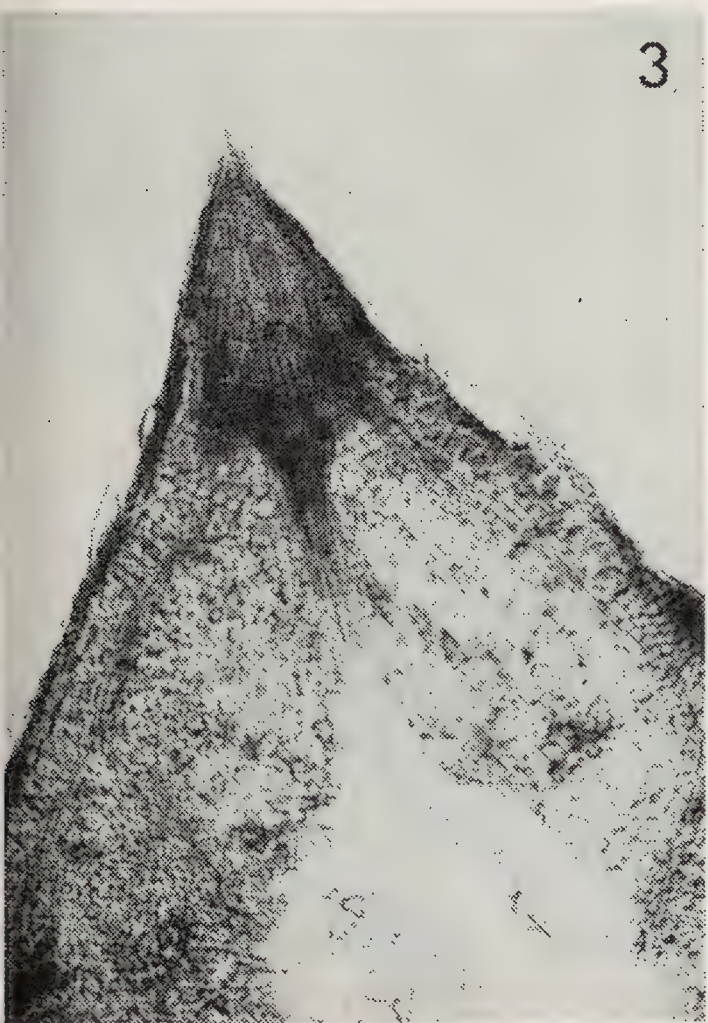
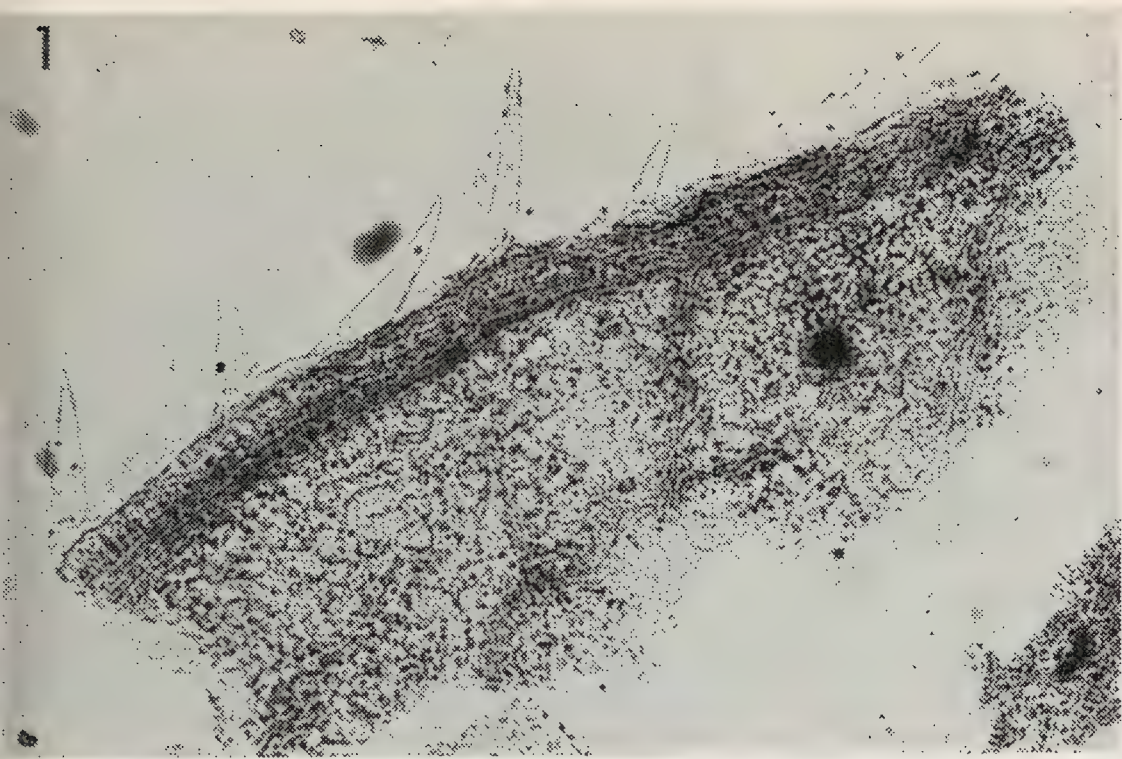
Field notes were made on the exact position and the type of plant on which each snail was collected. Although gut contents showed that some snails had been feeding on the same species of food plant to which they were attached, others showed no correlation between their position in the habitat and their previous meal. These had fed elsewhere. Many snails showed pieces of stem material (recognized by long narrow cells and the appropriate plant hairs) in the gut, and in some it was evident that fragments in the posterior half of the intestine represented pieces of stem which had been rasped as the snail travelled up the plant stem. Results of subsequent feeding on leaves were often evident in the crop. Wolda, Zweep and Schuitema 1971, also distinguished between the food plants and the daytime resting sites of *Cepaea nemoralis*: some favourite food plants were not popular resting sites.

The appearance of the nettle patch at Southridge changed dramatically during the course of the year. In winter the tall stems of the nettles were dead as a result of autumn frosts, leaving only small leafy shoots (5 cms) and many dead stems of nettles, cow parsley and hogweed from the previous summer. The only leafy growth was some grass, cow parsley, dead nettle and some very short shoots of stinging nettles. As a result faeces of snails taken on warm winter days, when some feeding had taken place, were pale brown in colour and consisted mostly of dead stem material. Faeces of *Monacha* from the same habitat in summer were frequently dark green in colour containing a high level of chlorophyll from leaves (Fig. 5). It appeared that the snails mostly fed on the older and slightly senescent leaves at the base of the stem. In captivity, when *M. cantiana* was presented with a stem of nettle, it would tend to feed on the older leaves and to avoid the very young leaves near the apex. This tendency has also been observed in *Arianta arbustorum* living amongst *Urtica dioica* and *Mercurialis perennis* in Derbyshire (Grime and Blythe, 1969). In the field situation, as snails often spend the daytime at ground level, it is the lower leaves which they reach first when they crawl up the plants to feed.

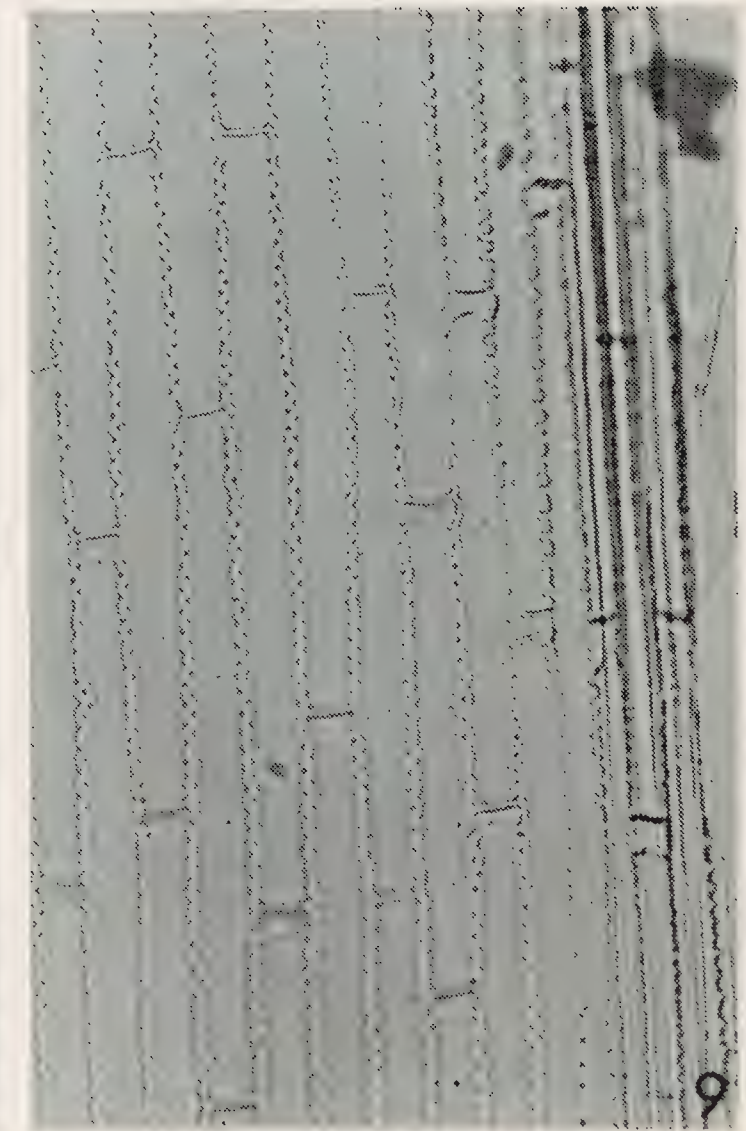
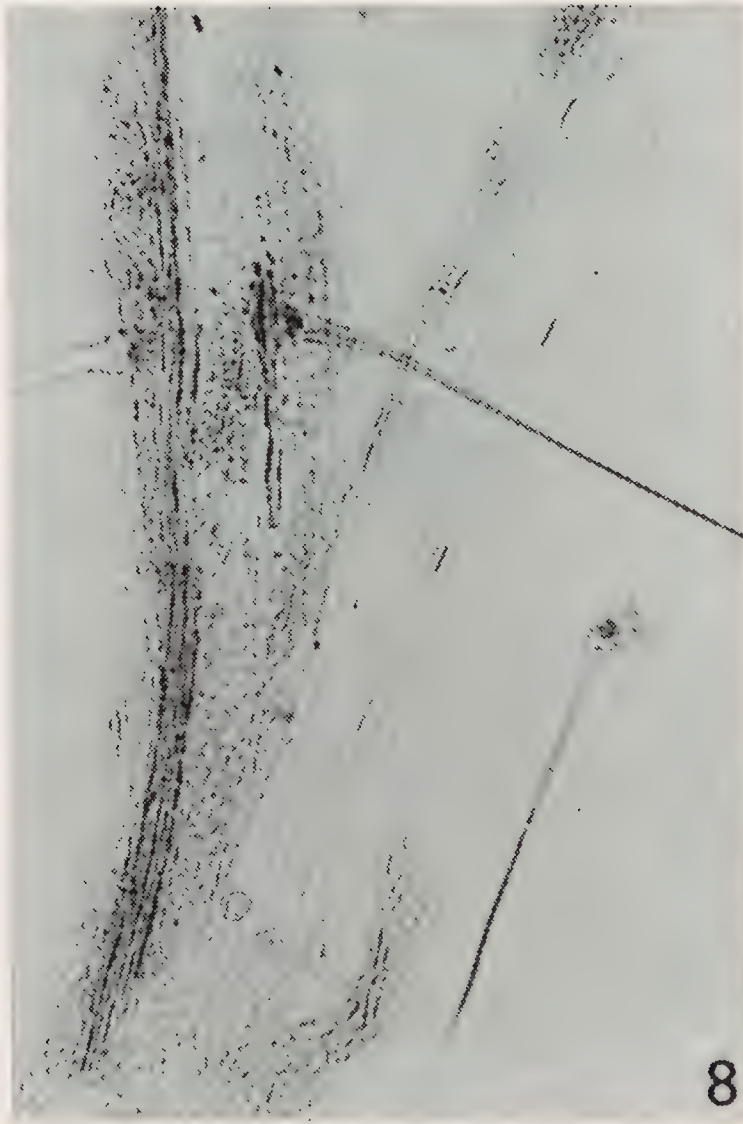
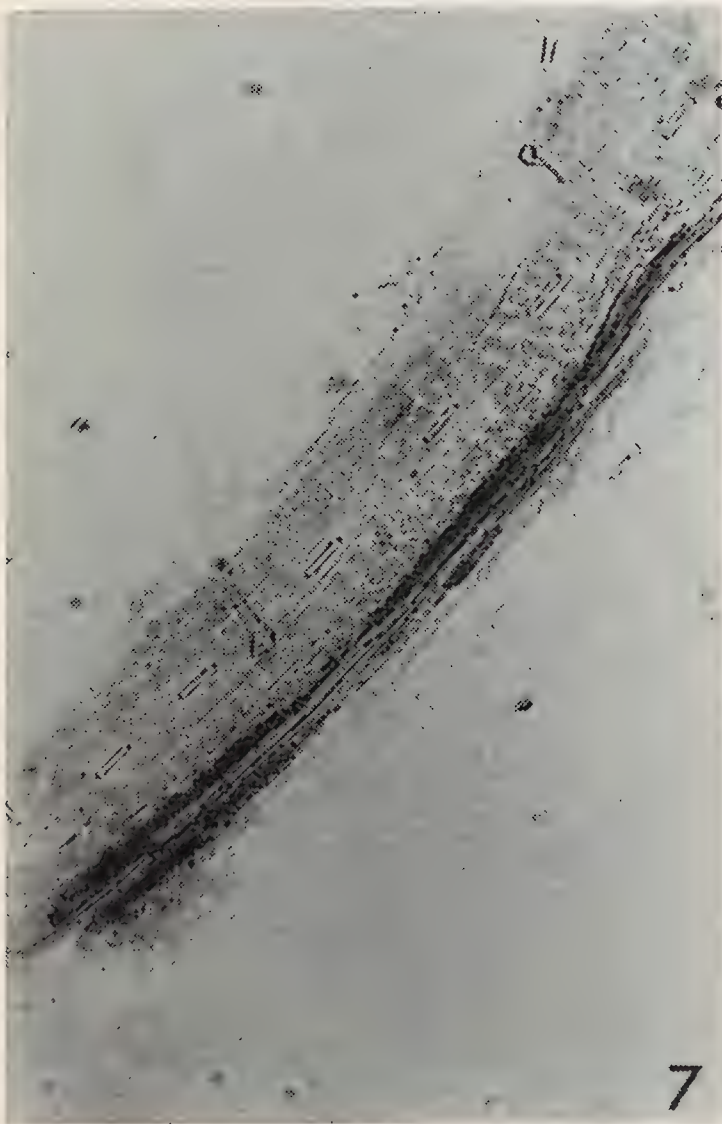
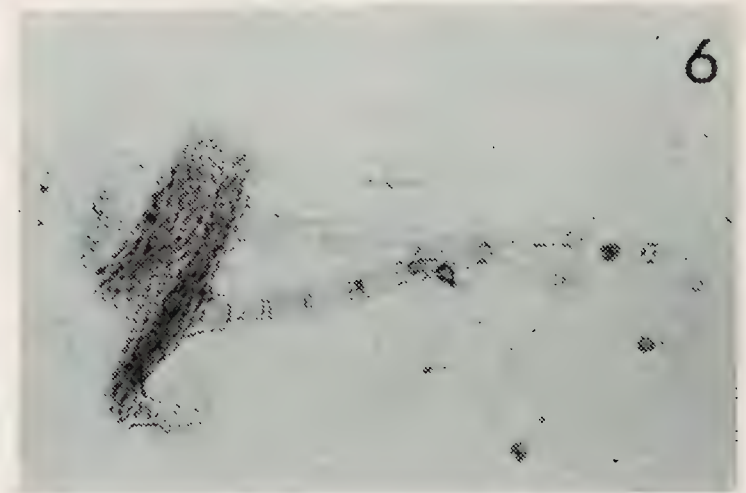
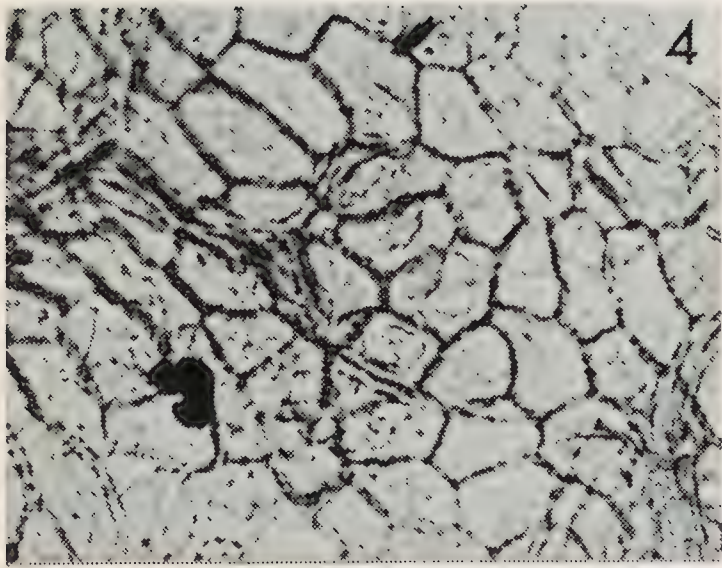
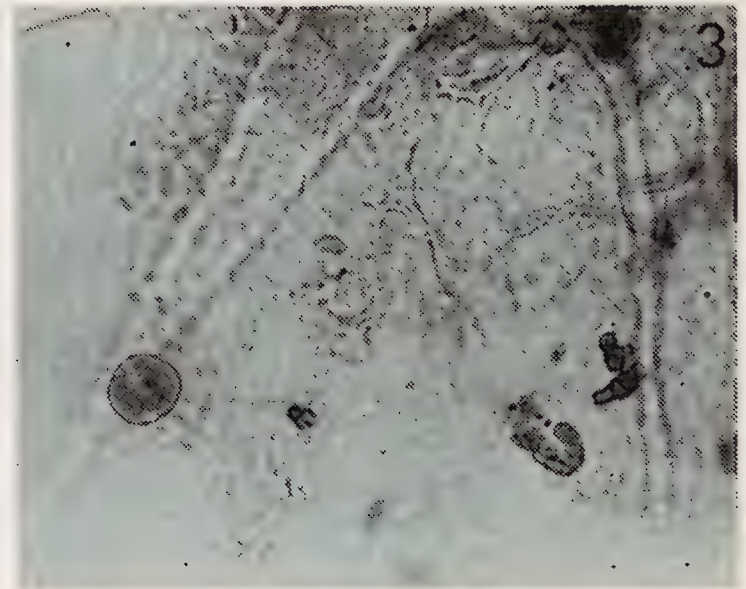
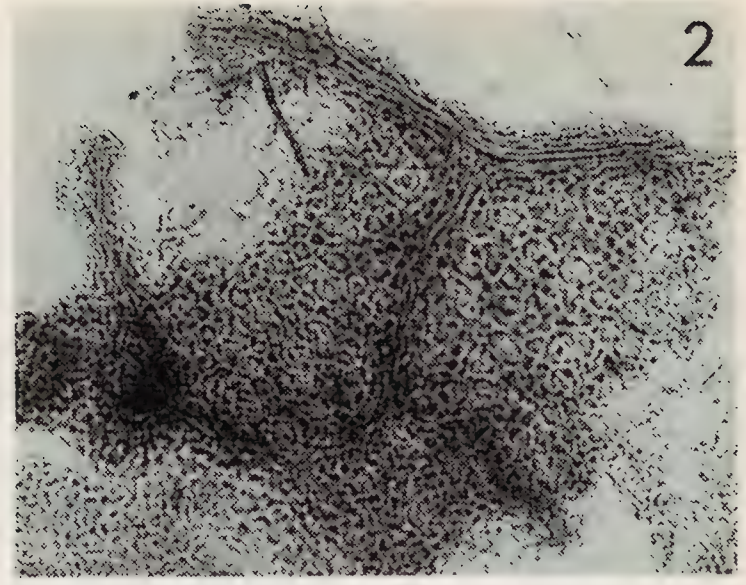
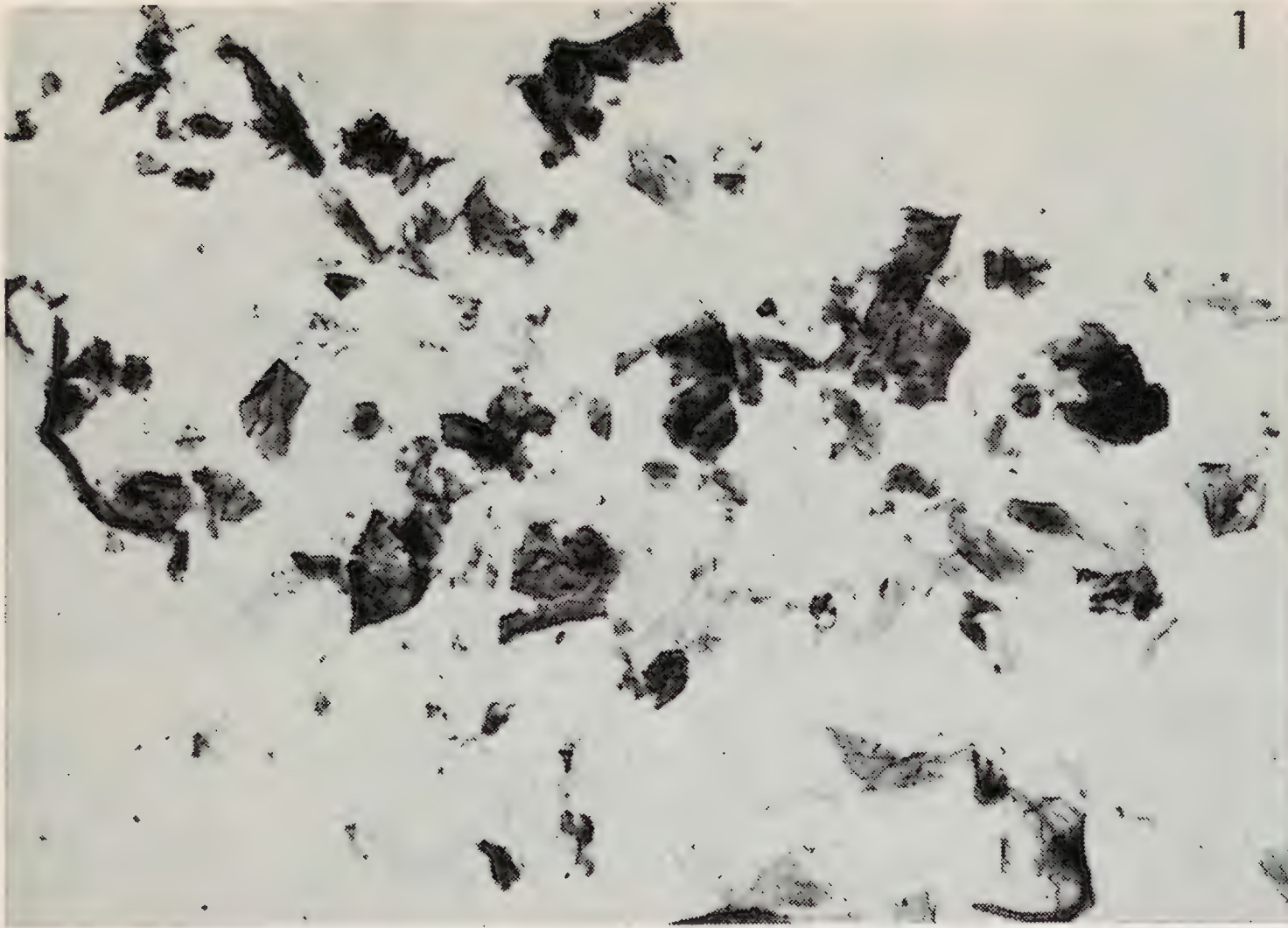
EXPLANATION OF PLATE 1 (Opposite)

Details of plant structures which were used in the identification of food substances of helioid snails. These photographs were taken from gut contents of *Monacha cantiana* collected from Play Hatch, Berkshire in March 1966. The only exception is Fig. 2 which was photographed from a standard mount of a leaf. The photographs were taken with a photomicroscope.

Fig. 1. The edge of a leaf of *Anthriscus sylvestris* showing plant hairs (trichomes) and vascular tissue. Fig. 2. Trichomes at the edge of a leaf of *Heracleum sphondylium*. Fig. 3. The apex of a leaf of *Anthriscus sylvestris*. Fig. 4. The tip of an undischarged stinging hair of *Urtica dioica*. Fig. 5. A stinging hair of *Urtica dioica* showing the multicellular base. Fig. 6. Ordinary trichomes of *Urtica dioica*. Fig. 7. Xylem vessels, probably from stem material. Fig. 8. Trichome of *Lamium album* showing the two segments. Fig. 9. Xylem vessels showing detail. Fig. 10. Cluster crystals or druses.



FOOD OF SNAILS



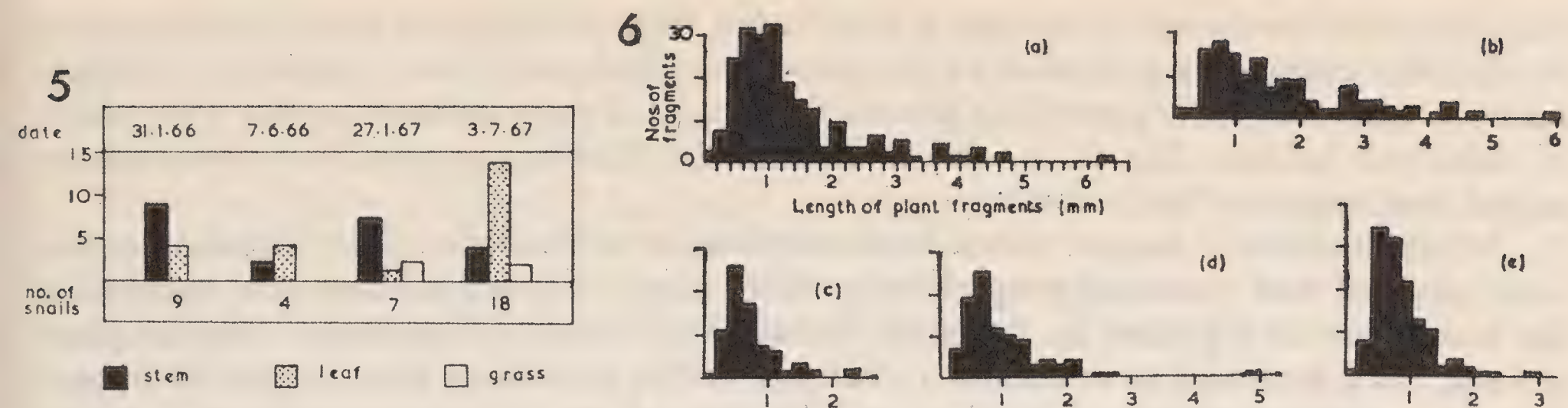


Fig. 5. The relative proportions of stem, leaf (of dicotyledons) and grass fragments in the gut of *Monacha cantiana* collected from Southridge, Berkshire. Two of the samples were taken in winter and two in summer.

Fig. 6. Histograms showing the length of plant fragments in the gut of *Monacha cantiana* collected from Play Hatch, March 1966. The snails had been feeding on:—(a) stem; (b) grass and other unidentified plants; (c) cow parsley; (d) grass and cow parsley; (e) cow parsley.

Examination of the gut contents of *Monacha* showed fragments of varying sizes. Some pieces of *Anthriscus sylvestris* and *Urtica dioica* included the entire thickness of the leaf and sometimes complete apices were found: these large pieces were very helpful in the identification of the food plants. Measurements were made of the lengths of fragments of food on selected microscope slides and the results of these are shown in Fig. 6. Pieces of stem and grass were generally long and narrow (up to 6 mm) whilst pieces of leaves of dicotyledon plants were usually square and not more than 3 mm in length. Some of these leaves, as a result of their structure appeared to be tackled by the snail in different ways. Those of the stinging nettle *Urtica dioica*, with a strong network of veins supporting convex sheets of leaf lamina were easily grasped by a snail feeding on the dorsal surface. More central pieces of nettle leaf were found in gut contents examined than were apices or edge pieces. In contrast the leaf veins of cow parsley, *Anthriscus sylvestris*, were not so strongly developed and the entire leaf divided and fern-like. The proportion of peripheral and apical areas on leaves of cow parsley was greater than on the simple leaf of stinging nettle. Leaf damage and fragments in the gut suggested that cow parsley was tackled by the snail from the edge of the leaf.

SELECTION OF FOOD BY SNAILS

On the roadside habitats studied, *Monacha cantiana* and *Hygromia striolata* fed on many of the plants in the community and stinging nettle and cow parsley, which were the most common plants, were also the major food plants for these two snails. In contrast, Grime,

EXPLANATION OF PLATE 2 (Opposite)

Details of plant structures which were used in the identification of food substances of helicid snails. Figs. 4 and 5 are from standard leaf preparations, the rest are from gut contents of snails. Fig. 1 is from *Monacha cantiana* collected at Southridge, Berkshire, in June 1966; Figs. 3, 6, 7 and 8 are from *M. cantiana* collected at Play Hatch, Berkshire, in March 1966, Fig. 9 from *M. cantiana* at the Ridgeway, Berkshire, in March 1967 and Fig. 2 from *Hygromia striolata* collected at Norbury Park, Surrey in April 1967. The photographs (with the exception of no. 1) were taken with a photomicroscope.

Fig. 1. A general view of gut contents of *Monacha cantiana* $\times 6$. Photo: E. Broadbent. Fig. 2. A fragment of a dead beech leaf (*Fagus sylvatica*) showing the pattern of vascular tissue. Fig. 3. The surface of a leaf of *Glechoma hederacea* showing a glandular cell (left) and fungal hyphae (right). Fig. 4. The epidermis of *Cirsium arvense* showing polygonal cells. Fig. 5. A spine from the leaf of *Cirsium arvense*. Fig. 6. A piece of *Glechoma hederacea* showing multisegmented trichomes. Figs. 7–8. Fragments of a grass leaf lamina showing the linear arrangement and elongate shape of the stomata, the unbranched pattern of vascular tissue and long slender trichomes. Fig. 9. Epidermis of *Brachypodium pinnatum* showing alternate long and short cells and the wavy margins of the cells.

MacPherson-Stewart and Dearman (1968) found that only 20% of the 52 native plants tested from calcareous grassland at Winnats Pass, Derbyshire were palatable to *Cepaea nemoralis*. However, it is interesting to note that many of the palatable species were plants of disturbed habitats like *Urtica dioica*. These latter findings suggest that there can be actual food selection by the snails.

Relatively little is known about food selection in snails although it is probable that both physical and chemical properties (possibly taste) of potential food are responsible for acceptance or rejection by the snail. Naturalists have long questioned whether plant hairs act as a deterrent to snails but Frömming (1934) could find no evidence to support this. In a series of experiments using fresh leaves and cut discs from leaves of a variety of plants with different physical characteristics, Grime, MacPherson-Stewart and Dearman (1968) could also find no evidence to suggest that hairs in general were an effective deterrent to feeding. The stinging nettle which is an important food plant for *Cepaea nemoralis*, *Arianta arbustorum*, *Monacha cantiana*, *Hygromia striolata* and *Agriolimax reticulatus* has a leaf with many curved spines (Fig. 4) and some large stinging hairs (Plate 1, figs. 4 and 5). Grime, Blythe and Thornton (1970) estimated the palatability of various plants using fresh leaves, leaf discs and aqueous extracts of leaves presented on discs of filter paper. Of the physical characteristics of the leaf they suggested that the large helioid snails *Cepaea* and *Arianta* could be put off by a hard exterior leaf surface, and this was particularly evident with some of the grasses. They also showed that some plant leaves of a low palatability would become acceptable as they became senescent. Field evidence of this showing a higher proportion of snail damage on the older leaves of stinging nettle and dogs mercury was described at the Winnats Pass (Grime and Blythe, 1969).

Experiments using aqueous leaf extract on filter paper demonstrated influence of the chemical nature of a plant leaf on its acceptance as a food plant by a snail. Water extracts of some plants including *Plantago lanceolata* L., *Scabiosa columbaria* L., *Lathyrus pratensis* L. and *Hedera helix* L. rendered filter paper unpalatable, thus demonstrating that the snail was able to distinguish some tastes in its food (Grime, MacPherson-Stewart and Dearman, 1968). Any possible resistance to feeding on stinging nettles was shown to be overcome by the odour of nettle which encouraged feeding in snails (Grime, Blythe and Thornton, 1970).

Feeding experiments on slugs have shown that many common weeds, again plants of disturbed habitats, are acceptable food for *Agriolimax reticulatus* and *Arion hortensis* (Duval, 1971 and 1973). Pallant (1969) set up some feeding experiments using food from a woodland habitat to compare with results of analyses of gut contents from the same site. In these experiments the slugs were given various choices of food. *Ranunculus repens* L. and *Urtica dioica*, which were the most common food plants in the gut contents, also ranked as first and second choice in the feeding experiments.

CONCLUSIONS

Although food is obviously a vital necessity of life for snails, Boycott (1934) did not consider it to be an important limiting factor for land snails since it is usually in excess and snails will accept a range of different foods. This opinion has recently been supported by Wolda, Zweep and Schuitema for *Cepaea* populations. Grime and Blythe (1969) did report higher densities of *Arianta arbustorum* in patches of stinging nettle than amongst adjacent plants where fewer palatable species were present, and similarly the highest densities of *Monacha cantiana* along two transect lines at Southridge were in the nettles (Chatfield, 1972). The favourable nature of these sites is evident from the large numbers of snails living there, but whether it is the food offered by the nettle or the physical environment or a combination of the two is not known. The nutritional quality of the

food can affect growth rates of snails (Chatfield, 1973 and Williamson, 1975) and it is possible that it may affect fecundity also. In a particularly favourable habitat there could be a greater rate of egg production which might be coupled with a high survival rate leading to a denser population.

Slugs and snails of disturbed habitats appear to be able to feed on a large proportion of the plants in their habitat. The ability to utilize a wide range of food is obviously an advantage to an animal, particularly in enabling it to cope with change in its environment, but more research is needed before we are in a position to review the effect of food on the way of life of slugs and snails.

Few people have considered the effect which slugs and snails, seemingly small and insignificant creatures, have on the total environment, or, in the terminology of modern ecology 'the ecosystem'. Land slugs and snails which feed on living plants can result in total destruction of their food plants (often seedlings in an agricultural situation) or, if the grazing is low, this could result in stimulation of further plant growth: the regular mowing of a lawn keeps the rate of growth of the grass higher than it would otherwise be. Possibly the most significant effect on the ecosystem is rendered by species which feed on dead plant material. All plant growth results in a pile-up of dead litter at some time. Slugs and many of the snails feed on dead plants, breaking them down into small pieces. Some of the energy locked up in the leaf litter is utilized by the snail to sustain its own activities and growth. Mason (1970) estimated that snails feeding on plant matter actually assimilate about 50% of the food which they take in, and the remaining 50% of plant fragments are expelled, wrapped up in mucus in the faecal string. These particles are smaller than they were in the original state, before being broken up by the radula and jaw, and they are coated in mucus secreted by the gut of the snail. Snail faeces thus make attractive food for small creatures like some mites and millipedes which live in the leaf litter and these in their turn further break up the leaf fragments. Leaf litter which has been through the intestine of animals is further broken down by fungi and microbial organisms in the litter. In this way, the energy locked up in the dead leaves is used by various organisms, and inorganic chemicals like phosphates, nitrates and calcium salts, etc. are returned to the soil where they are available once more as plant nutrients. The concepts of energy flow and the circulation of inorganic materials are explained in many modern ecology textbooks (Odum, 1963; Phillipson, 1971). Mason has estimated that a snail population in a woodland can consume 0.35–0.43% of the total weight of leaf litter in the wood. Mason's study was restricted to snails, but if one took slugs into consideration also, the percentage of leaf litter consumed by the molluscs would be considerably more. Slugs are larger animals than most woodland snails, and thus their food consumption would be greater. In any case the Mollusca are only part of the total fauna which is involved in the breakdown of litter.

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A NOMENCLATURAL LIST OF THE LAND MOLLUSCA OF THE BRITISH ISLES

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Abstract: A revised and updated nomenclatural list of British land Mollusca is presented together with comments on critical points.

For a long time there has been a very stable nomenclatural tradition in British malacology. This has obvious advantages. Only a limited number of novelties in taxonomy, and subsequent nomenclature, prove to be well founded. It is advisable to incorporate them in handbooks only after critical scrutiny. Furthermore, it is only when nomenclature remains stable for a fairly long period that a field like malacology can be open for the broad participation of amateurs, instead of being restricted to specialists. A project like the mapping scheme for British non-marine Mollusca—unrivalled anywhere in the world—which is now entering a new phase, is essentially based on a well organized co-operation of volunteers, and could never have been effected without a stable and well-known nomenclature.

A stable nomenclature, however, has certain drawbacks. It means a conservative nomenclature, some elements of which can become out-of-date or definitely misleading. One must also bear in mind that this stable tradition is confined to the British Isles; other countries have other traditions. For broad international co-operation to be effective it is necessary for nomenclature in different countries to be revised mutually so that a common standard may be achieved. In principle everyone is agreed upon this point.

Now seems to be an appropriate time to bring British nomenclature into line with international standards. As mentioned above, the new mapping scheme is now reaching its first fruition and it is expected that the results will soon be published. When this takes place an epoch of direct extension of the knowledge of distribution, which can be said to have started with the first entry in the Conchological Society's Census record books on 12 October 1876, will have been accomplished. In future interest will probably be more directed to general European distribution, especially as the preliminaries of a European mapping scheme are already in progress. Henceforth there will be less use for 'domestic' names.

SPECIES LIST

ORDER	FAMILY	SPECIES	OPINION No.	LIST No.
Prosobranchia				
	Pomatiidae	<i>Pomatias elegans</i> (Müller 1774)		
	Assimineidae	<i>Assiminea grayana</i> Fleming 1828		
	Aciculidae	<i>Acicula fusca</i> (Montagu 1803)	336	356

Euthyneura

Ellobiidae	<i>Carychium minimum</i> Müller 1774	335	306
	<i>Carychium tridentatum</i> (Risso 1826)		
	<i>Ovatella</i> (<i>Myosotella</i>) <i>myosotis</i> (Draparnaud 1801)		
Succineidae	<i>Catinella</i> (<i>Quickella</i>) <i>arenaria</i> (Bouchard-Chantereaux 1837)	336	331
	<i>Succinea</i> (<i>Succinea</i>) <i>putris</i> (Linnaeus 1758)	336	395
	<i>Succinea</i> (<i>Succinella</i>) <i>oblonga</i> Draparnaud 1801	336	382
	1.) <i>Oxyloma pfeifferi</i> (Rossmässler 1835)		
	<i>Oxyloma sarsi</i> (Esmark 1886)		
Cochlicopidae	2.) <i>Azeca goodalli</i> (Férussac 1821)	335	318
	<i>Cochlicopa lubrica</i> (Müller 1774)	336	372
	3.) <i>Cochlicopa lubricella</i> (Porro 1838)		
Pyramidulidae	<i>Pyramidula rupestris</i> (Draparnaud 1801)	335	314
Vertiginidae	<i>Columella edentula</i> (Draparnaud 1805)	336	350
	<i>Columella aspera</i> Waldén 1966		
	4.) <i>Columella</i> forma aberr.		
	<i>Truncatellina cylindrica</i> (Férussac 1807)	336	345
	5.) <i>Truncatellina callicratis britannica</i> Pilsbry 1920		
	<i>Vertigo</i> (<i>Vertigo</i>) <i>pusilla</i> Müller 1774	335	312
	<i>Vertigo</i> (<i>Vertigo</i>) <i>antivertigo</i> (Draparnaud 1801)	336	330
	<i>Vertigo</i> (<i>Vertigo</i>) <i>substriata</i> (Jeffreys 1833)	336	415
	<i>Vertigo</i> (<i>Vertigo</i>) <i>pygmaea</i> (Draparnaud 1801)	336	397
	<i>Vertigo</i> (<i>Vertigo</i>) <i>moulinsiana</i> (Dupuy 1849)	336	377
	<i>Vertigo</i> (<i>Vertigo</i>) <i>lilljeborgi</i> (Westerlund 1871)	336	371
	<i>Vertigo</i> (<i>Vertigo</i>) <i>alpestris</i> Alder 1838	336	327
	<i>Vertigo</i> (<i>Vertigo</i>) <i>geyeri</i> Lindholm 1925		
	<i>Vertigo</i> (<i>Vertilla</i>) <i>angustior</i> Jeffreys 1830	336	329
Chondrinidae	<i>Abida secale</i> (Draparnaud 1801)	335	315
Pupillidae	<i>Pupilla</i> (<i>Pupilla</i>) <i>muscorum</i> (Linnaeus 1758)	335	319
	<i>Leiostyla</i> (<i>Leiostyla</i>) <i>anglica</i> (Wood 1828)	336	328
	<i>Lauria</i> (<i>Lauria</i>) <i>cylindracea</i> (Da Costa 1778)	335	316
	<i>Lauria</i> (<i>Lauria</i>) <i>sempronii</i> (Charpentier 1837)		
Valloniidae	<i>Vallonia costata</i> (Müller 1774)	336	342
	<i>Vallonia pulchella</i> (Müller 1774)	335	323
	<i>Vallonia excentrica</i> Sterki 1892		
	<i>Acanthinula aculeata</i> (Müller 1774)	335	293
	<i>Spermodea lamellata</i> (Jeffreys 1830)	336	367
Pleurodiscidae	* <i>Pleurodiscus balmei</i> (Potiez and Michaud 1838)		
Enidae	<i>Ena</i> (<i>Ena</i>) <i>montana</i> (Draparnaud 1801)	475	1302
	<i>Ena</i> (<i>Ena</i>) <i>obscura</i> (Müller 1774)	475	1303
Endodontidae	<i>Punctum</i> (<i>Punctum</i>) <i>pygmaeum</i> (Draparnaud 1801)	336	396
	*6.) <i>Helicodiscus</i> (<i>Helicodiscus</i>) <i>parallelus</i> (Say 1821)	336	385
	* <i>Helicodiscus</i> (<i>Hebetodiscus</i>) cf. <i>singleyanus</i> Pilsbry		
	<i>Discus</i> (<i>Discus</i>) <i>rotundatus</i> (Müller 1774)	336	404
Arionidae	<i>Geomalacus maculosus</i> Allman 1843	335	305
	<i>Arion</i> (<i>Arion</i>) <i>ater</i> (Linnaeus 1758)	335	295
	7.) <i>Arion</i> (<i>Arion</i>) <i>rufus</i> (Linnaeus 1758)		
	<i>Arion</i> (<i>Arion</i>) <i>lusitanicus</i> Mabilie 1868		
	8.) <i>Arion</i> (<i>Mesarion</i>) <i>subfuscus</i> (Draparnaud 1805)	336	413
	<i>Arion</i> (<i>Carinarion</i>) <i>circumscribed</i> Johnston 1828	336	338
	<i>Arion</i> (<i>Carinarion</i>) <i>silvaticus</i> Lohmander 1937		
	<i>Arion</i> (<i>Carinarion</i>) <i>fasciatus</i> (Nilsson 1823)		
	9.) <i>Arion</i> (<i>Kobeltia</i>) <i>hortensis</i> Férussac 1819	336	361
	10.) <i>Arion</i> (<i>Kobeltia</i>) <i>intermedius</i> Normand 1852	336	364
Vitrinidae	<i>Vitrina</i> (<i>Vitrina</i>) <i>pellucida</i> (Müller 1774)	336	388
	<i>Semilimax</i> (<i>Semilimax</i>) <i>pyrenaicus</i> (Férussac 1821)	336	399
	<i>Phenacolimax</i> (<i>Phenacolimax</i>) <i>major</i> (Férussac 1807)	336	373
Zonitidae	*11.) <i>Hawaiiia minuscula</i> (Binney 1840)	336	376
	<i>Vitrea</i> (<i>Subrimatus</i>) <i>subrimata</i> (Reinhardt 1871)		
	<i>Vitrea</i> (<i>Crystallus</i>) <i>crystallina</i> (Müller 1774)	336	344
	<i>Vitrea</i> (<i>Crystallus</i>) <i>contracta</i> (Westerlund 1871)		
	<i>Nesovitrea</i> (<i>Perpolita</i>) <i>hammonis</i> (Ström 1765)	937	2422

WALDEN: LIST OF BRITISH LAND MOLLUSCA

		<i>Aegopinella pura</i> (Alder 1830)	336	394
	12.)	<i>Aegopinella nitidula</i> (Draparnaud 1805)	336	381
		<i>Oxychilus</i> (<i>Oxychilus</i>) <i>draparnaudi</i> (Beck 1837)	336	348
		<i>Oxychilus</i> (<i>Oxychilus</i>) <i>cellarius</i> (Müller 1774)	431	1045
		<i>Oxychilus</i> (<i>Ortizius</i>) <i>alliarius</i> (Miller 1822)	336	326
		<i>Oxychilus</i> (<i>Ortizius</i>) <i>helveticus</i> (Blum 1881)		
		<i>Zonitoides</i> (<i>Zonitellus</i>) <i>excavatus</i> (Alder 1830)	336	353
	*	<i>Zonitoides</i> (<i>Zonitellus</i>) <i>arboreus</i> (Say 1816)		
		<i>Zonitoides</i> (<i>Zonitoides</i>) <i>nitidus</i> (Müller 1774)	335	308
Milacidae	13.)	<i>Milax</i> (<i>Milax</i>) <i>gagates</i> (Draparnaud 1801)	335	302
	*14.)	<i>Milax</i> (<i>Milax</i>) <i>nigricans</i> (Schultz in Phillipi 1836)		
		<i>Milax</i> (<i>Milax</i>) <i>sowerbyi</i> (Férussac 1823)	336	409
		<i>Milax</i> (<i>Milax</i>) <i>budapestensis</i> (Hazay 1881)		
	*	<i>Boettgerilla pallens</i> Simroth 1912		
Limacidae		<i>Limax</i> (<i>Limax</i>) <i>maximus</i> Linnaeus 1758	336	375
		<i>Limax</i> (<i>Limax</i>) <i>cinereoniger</i> Wolf 1803	336	337
		<i>Limax</i> (<i>Limacus</i>) <i>flavus</i> Linnaeus 1758	336	354
	15.)	<i>Limax</i> (<i>Limacus</i>) <i>grossui</i> Lupu 1970		
		<i>Limax</i> (<i>Malacolimax</i>) <i>tenellus</i> Müller 1774	336	417
	*16.)	<i>Limax</i> (<i>Lehmannia</i>) <i>nyctelius</i> Bourguignat 1861		
		<i>Limax</i> (<i>Lehmannia</i>) <i>marginatus</i> Müller 1774		
	*	<i>Limax</i> (<i>Lehmannia</i>) <i>valentianus</i> Férussac 1823		
		<i>Deroceras</i> (<i>Deroceras</i>) <i>laeve</i> (Müller 1774)		
		<i>Deroceras</i> (<i>Agriolimax</i>) <i>agreste</i> (Linnaeus 1758)		
		<i>Deroceras</i> (<i>Agriolimax</i>) <i>reticulatum</i> (Müller 1774)	336	402
	17.)	<i>Deroceras</i> (<i>Malino</i>) sp.		
Euconulidae		<i>Euconulus</i> (<i>Euconulus</i>) <i>fulvus</i> (Müller 1774)	335	301
		<i>Euconulus</i> (<i>Euconulus</i>) <i>alderi</i> (Gray 1840)		
Ferussaciidae		<i>Ceciloides</i> (<i>Ceciloides</i>) <i>acicula</i> (Müller 1774)	335	292
Subulinidae	*18.)	<i>Subulina octona</i> (Bruguière 1789)	335	309
	*	<i>Subulina striatella</i> (Rang 1831)		
	*19.)	<i>Lamellaxis</i> (<i>Allopeas</i>) <i>clavulinus</i> (Potiez and Michaud 1838)		
	*	<i>Opeas pumilium</i> (L. Pfeiffer 1840)		
Clausiliidae		<i>Cochlodina</i> (<i>Cochlodina</i>) <i>laminata</i> (Montagu 1803)	336	368
	20.)	<i>Macrogastra rolpheii</i> (Turton 1826)	336	403
		<i>Clausilia</i> (<i>Clausilia</i>) <i>bidentata</i> (Ström 1765)		
		<i>Clausilia</i> (<i>Clausilia</i>) <i>dubia</i> Draparnaud 1805	336	349
		<i>Laciniaria</i> (<i>Alinda</i>) <i>biplicata</i> (Montagu 1803)	336	334
		<i>Balea perversa</i> (Linnaeus 1758)	335	322
Testacellidae		<i>Testacella</i> (<i>Testacella</i>) <i>maugei</i> Férussac 1819		
		<i>Testacella</i> (<i>Testacella</i>) <i>haliotidea</i> Draparnaud 1801		
		<i>Testacella</i> (<i>Testacella</i>) <i>scutulum</i> Sowerby 1821	336	406
Streptaxidae	*21.)	<i>Gulella</i> (<i>Huttonella</i>) <i>io</i> Verdcourt 1974		
Bradybaenidae		<i>Bradybaena</i> (<i>Bradybaena</i>) <i>fruticum</i> (Müller 1774)		
Helicidae	22.)	<i>Candidula intersecta</i> (Poiret 1801)		
		<i>Candidula gigaxii</i> (L. Pfeiffer 1850)	336	357
	23.)	<i>Cernuella</i> (<i>Cernuella</i>) <i>virgata</i> (Da Costa 1778)	336	423
		<i>Helicella</i> (<i>Helicella</i>) <i>itala</i> (Linnaeus 1758)	431	1046
	*	<i>Trochoidea</i> (<i>Trochoidea</i>) <i>elegans</i> (Gmelin 1791)	336	351
		<i>Cochlicella acuta</i> (Müller 1774)		
		<i>Monacha</i> (<i>Monacha</i>) <i>cartusiana</i> (Müller 1774)	431	1044
		<i>Monacha</i> (<i>Monacha</i>) <i>cantiana</i> (Montagu 1803)	336	335
		<i>Ashfordia granulata</i> (Alder 1830)	336	359
		<i>Zenobiella</i> (<i>Zenobiella</i>) <i>subrufescens</i> (Miller 1822)	336	414
		<i>Hygromia cinctella</i> (Draparnaud 1801)	335	296
		<i>Hygromia limbata</i> (Draparnaud 1805)		
		<i>Trichia</i> (<i>Trichia</i>) <i>striolata</i> (C. Pfeiffer 1828)	336	412
	24.)	<i>Trichia</i> (<i>Trichia</i>) <i>plebeia</i> (Draparnaud 1805)		
		<i>Trichia</i> (<i>Trichia</i>) <i>hispida</i> (Linnaeus 1758)	336	360
		<i>Ponentina subvirescens</i> (Bellamy 1839)	336	416
		<i>Helicodonta obvoluta</i> (Müller 1774)	336	383
		<i>Arianta arbustorum</i> (Linnaeus 1758)	335	294
		<i>Helicigona lapicida</i> (Linnaeus 1758)	336	369

<i>Theba pisana</i> (Müller 1774)	431	1047
<i>Cepaea nemoralis</i> (Linnaeus 1758)	336	380
<i>Cepaea hortensis</i> (Müller 1774)	336	362
25.) <i>Helix</i> (<i>Cornu</i>) <i>aspersa</i> Müller 1774	336	332
<i>Helix</i> (<i>Helix</i>) <i>pomatia</i> Linnaeus 1758	336	392

NOTES

The present list essentially follows the system given by Zilch 1959–60 (*Handbuch der Paläozoologie* 6: 2), though in addition subsequent progress in taxonomy is considered. The most striking difference is that the family Succineidae has been placed in its traditional position as the most primitive Stylommatophora, as a consequence of the strong evidence given by Patterson, 1971 (*Malac. Review* 4: 131–202).

In the formal aspect the author has mentioned subgenera throughout, when a genus is split up into such, even if only one subgenus is represented in the British fauna. On the other hand subspecific division is not considered. Even if the British form does not represent the nominate race (as is the case with *Clausilia dubia*) only the specific name has been used. The only exception is *Truncatellina callicratis britannica*, for the reasons considered in the note.

As the major aim of the present list is to give an account of the present state of nomenclature, which is not primarily categorical but sound and revealing, the basis upon which it rests must also be considered. Therefore all cases of names placed on the Official List of Specific Names in Zoology are recognized, and furthermore all problematic cases are referred to in notes.

A special problem arises in deciding which species should be included. The border between greenhouse aliens, adventives and accidentally introduced species, which have perhaps not survived even as individuals, can never be drawn exactly. The author has strived to include only those species which, judging from the literature, seem to have an established occurrence in the country, and to spread and perpetuate freely (even if only under sheltered conditions, e.g. in greenhouses). Some species, which have apparently died out, have been excluded. However, the author is aware that the choice of species will certainly be open to criticism. For further information see Ellis 1951 (*J. Conch., Lond.* 23: 200).

Greenhouse aliens, as well as other introduced species which still maintain the character of a foreign element in the British fauna are marked with an asterisk.

1.) a. The name *elegans* (Risso 1826) has been avoided here, because its meaning is ambiguous. Quick 1933 (*Proc. malac. Soc. Lond.* 20: 295–318) restricted this name to a species which has later been proved to be identical with *sarsi* (Esmark 1886) by Odhner 1949 (*Vidensk. Medd. Dansk. naturh. Foren.* 3: 217–224). It has also been shown that *elegans* (Risso) is identical with *pfeifferi* (Rossmässler), the former name having priority. As *elegans* has been used extensively in both meanings great confusion has arisen. The only way to end this is to reject this name, and maintain the indisputable names *pfeifferi* and *sarsi*. The question will probably be submitted to the ICZN.

b. For the reasons for following Zilch (1959–60) in admitting *Oxyloma* generic rank, see Patterson 1971 (*Malac. Review* 4: 131–202).

2.) Synonym *menkeana* (C. Pfeiffer 1821). Cf. Paul 1974 (*J. Conch., Lond.* 28: 155–172).

3.) A third species, *C. repentina*, has been described by Hudec 1960 (*Acta Acad. Sci. Cechoslov. Basis Brunensis* 32: 287), but it is still a matter of dispute if this has an objective existence, or if it is based on intermediate specimens of either of the other species. Both show considerable variation. However, there does not seem to be any evidence of a distinct third species in Britain, even if intermediate and not accurately determinable specimens occur.

4.) A small, anomalous form has been found in western Ireland, the taxonomic position of which is problematic. It is very similar to the North American *C. simplex* (Gould 1841), a form which is also not accurately understood. More or less identical specimens have been found in Iceland, where typical *edentula* and *aspera* also exist.

5.) There is scarcely any doubt that *T. britannica* is conspecific with the Continental species usually known as *T. strobili* (Gredler 1853), as assumed by Pilsbry in the original description. In contrast with the highly variable Continental form, *britannica* is fairly uniform, characterized by its relatively short shell and weak dentition.

A distinctive feature seems to be that in *britannica* the palatal denticle is the first one to be reduced, followed by the parietal denticle, thus leaving only the columellar tooth. Even this can be fairly inconspicuous. Actually, most specimens have only the columellar tooth present. In the main form (*strobili* auctt.) the columellar tooth is usually reduced first, and the palatal denticle remains as the last. It is likely that this difference has a genetic basis. For these reasons it is justified to maintain *britannica* as a subspecies even if similar specimens can occasionally be found on the Continent.

Concerning the nominate species, Forcart 1965 (*Verhandl. Naturf. Ges. Basel.* 78: 84) has stated that *callicratis* (Scacchi 1833) has to be considered as a senior synonym to *strobili*. A biometrical study on the

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extensive material of Favre 1927 (*Mém. Soc. Phys. Hist. nat. Genève* **40** (3): 174–434), and on material from the original locality of *callicratis* (in coll. Westerlund, Göteborg Museum), carried out by the present author, has confirmed this view.

6.) No published British records since 1911, but museum material exists which seems to be of a more recent origin.

7.) Some authors maintain that *rufus* is a subspecies of *ater*, though the evidence is not conclusive. The significant differences are in the genital anatomy, but as there is some overlap, conclusions cannot always be drawn from single dissected specimens. In the vast majority of specimens the anatomical characters are quite distinct. Cf. Quick 1960 (*Bull. Br. Mus. nat. Hist. (Zool.)* **6**: 146).

8.) *A. subfuscus* shows a complicated subspecific taxonomy. It is not excluded that further research will show that an aggregate species is involved.

9.) There is strong evidence that British *A. hortensis* is an aggregate of three species. A study is in progress by Miss S. M. Davies, S. Croydon.

10.) *A. intermedius* was placed in the section *Micrarion* by Hesse 1926. This is not sufficiently differentiated from *Kobeltia* to be regarded as a distinct subgenus.

11.) As for *H. parallelus*, no records have been published since 1911, but material which seems to be of more recent origin exists.

12.) Forcart 1957 (*Mitt. Naturf. Ges. Bern* (NF) **15**: 203) draws attention to the fact that the original lot of *Helix nitidula* (in the Natural History Museum, Vienna) does not contain authentic *A. nitidula* auctt. However, the name has been interpreted in accordance with Rossmässler 1835 (*Iconographie* **1**: 72) for 140 years and it is this species which lives in the British Isles. There is no doubt that the name should be maintained in its current meaning, according to ICZN 23: b.

13.) It is not unequivocal that British *M. gagates* is identical with the species originally described under this name. Cf. Quick 1960 (*Bull. Br. Mus. nat. Hist. (Zool.)* **6**: 150).

14.) Synonym *M. insularis* (Lessona and Pollonera 1882). Cf. Giusti 1968 (*Memorie Soc. Tosc. Sci. nat.* **B75**: 265–324).

15.) See *J. Conch., Lond* **29**:1.

16.) *L. nyctelius* has features in common with both the subgenera *Lehmannia* and *Malacolimax*, and consequently it is scarcely possible to draw a sharp border between these subgenera. For further reasons for regarding *Lehmannia* as a subgenus of *Limax* see Waldén 1961 (*Ark. Zool. Ser. 2*, **15**: 85).

A species identified as *L. nyctelius* has recently been found to be widespread in SE Europe (Wiktor 1973, *Monogr. Fauny Polski* **1**, and Grossu and Lupu 1963, *Arch. Molluskenk.* **92**: 141–143). To what extent this is identical with Bourguignat's species from Algeria is not quite clear. The case should be considered with regard to the identity of the species found in the British Isles.

17.) Synonym *Deroceras caruanae* (Pollonera 1891). The correct name for the Mediterranean species is not yet certain. A note on this species will appear in a future issue of *J. Conch., Lond.*

18 and 19.) Recent records from 1962.

20.) a. The currently used generic name, *Iphigena* Gray 1821, is a *nomen nudum*.

b. The earliest reference for *rolphii*, Turton 1826 (*Zool. J.* **2**: 564–567) was not considered when the reference from 1831 was given under name No. 403 in the Official List of Specific Names in Zoology. The attention of the secretary of ICZN has been drawn to the case.

21.) Previously recorded as *G. devia* Conolly 1931.

22.) Synonym *Candidula caperata* (Montagu 1803). Poiret's earlier description of *C. intersecta* (Coquille *Aisne*, p. 79) is, however, distinct and unmistakable. No other species, living in the area concerned, can be involved.

23.) The single introduced British colony of the congeneric *C. (Xerocincta) neglecta* (Draparnaud 1805) was extirpated in 1922.

24.) Until now recorded under the name *Trichia liberta* (Westerlund 1870). This, however, was based on a form of *T. hispida* from Sweden. Recent work, still in progress, by C. R. C. Paul indicates that authentic *T. plebeia* (= *sericea sensu* Draparnaud 1801, non *sericea* Müller 1774) lives in England.

25.) The type of *Cornu copiae* Born 1778, a scalariform specimen of *H. aspersa*, is still present in the Vienna Museum (O. Paget *in litt.*). Consequently, *Cornu* has priority over *Cryptomphalus* Charpentier 1837, as a subgeneric name.

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A LIST OF THE FRESH AND
BRACKISH-WATER MOLLUSCA OF THE
BRITISH ISLES

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(Read before the Society, 18 October 1975)

Abstract: A provisional nomenclatural list of British freshwater molluscs is presented together with comments on critical points.

The following list is in no sense authoritative. It is offered merely as a complement to Dr. Waldén's revision of the land Mollusca (see p. 21), so that all our non-marine species are provisionally covered. Greenhouse aliens have been omitted. The need for a new list has arisen in connection with the Society's forthcoming *Atlas of the non-marine Mollusca of the British Isles*. Biological nomenclature is a language, and it was felt that the adoption in the *Atlas* of a more internationally familiar taxonomy than the one to which we have become accustomed would make the work more accessible to malacologists in other countries. References are given to the Opinions of the ICZN where specific names are on the *Official List*; otherwise the names and arrangement suggested below represent no more than a consensus of current ideas. A number of points of disagreement still exist and attention is drawn to some of these in the notes. Changes chiefly affect the names of genera, where there has been a tendency for an upgrading of taxa previously regarded only as subgenera, as for example in the Planorbidae. This is a somewhat subjective process, about which there can be no finality. In a few cases where the present specific names differ from those used in Ellis's *British Snails* (1926, and revised edition 1969) or in the 1951 non-marine Census List (*J. Conch.*, Lond. 23: 177) the alternatives are given in parentheses.

I am greatly indebted to Mr. Ellis for his comments and advice. Help was also received from Dr. Hubendick (Göteborg), Mr. Kuiper (Paris) and Mr. Melville (London).

SPECIES LIST

CLASS, ORDER	FAMILY	SPECIES	OPINION No.	LIST No.
Gastropoda, Prosobranchia				
	Neritidae	<i>Theodoxus fluviatilis</i> (Linnaeus 1758)	335	317
	Viviparidae	<i>Viviparus viviparus</i> (Linnaeus 1758)	573	1682
		<i>Viviparus contectus</i> (Millet 1813)	573	1683
		(= <i>V. fasciatus</i> auctt., non Müller)		
	Valvatidae	<i>Valvata</i> (<i>Valvata</i>) <i>cristata</i> Müller 1774	335	298
		1.) <i>Valvata</i> (<i>Cincinna</i>) <i>macrostoma</i> Mörch 1864		
		<i>Valvata</i> (<i>Cincinna</i>) <i>piscinalis</i> (Müller 1774)	336	391
	Hydrobiidae	2.) <i>Hydrobia</i> (<i>Hydrobia</i>) <i>ventrosa</i> (Montagu 1803)		

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	<i>Hydrobia (Hydrobia) neglecta</i> Muus 1963		
	<i>Hydrobia (Peringia) ulvae</i> (Pennant 1777)	336	419
	<i>Pseudamnicola confusa</i> (Frauenfeld 1863)		
	<i>Potamopyrgus jenkinsi</i> (E. A. Smith 1889)		
	<i>Marstoniopsis scholtzi</i> (A. Schmidt 1856)		
	(= <i>Bythinella steinii</i> (Martens), <i>Amnicola taylori</i> (E. A. Smith))		
Bithyniidae	<i>Bithynia tentaculata</i> (Linnaeus 1758)	475	1301
	<i>Bithynia leachii</i> (Sheppard 1823)		
Assimineidae	<i>Assiminea grayana</i> Fleming 1828		
Euthyneura			
Ellobiidae	3.) <i>Ovatella (Myosotella) myosotis</i> (Draparnaud 1801)		
	4.) <i>Leucophytia bidentata</i> (Montagu 1808)		
Physidae	<i>Aplexa hypnorum</i> (Linnaeus 1758)	335	303
	<i>Physa fontinalis</i> (Linnaeus 1758)	336	355
	5.) <i>Physa acuta</i> Draparnaud 1805	336	324
	<i>Physa heterostropha</i> Say 1817		
	<i>Physa gyrina</i> Say 1821		
6.) Lymnaeidae	<i>Lymnaea (Galba) truncatula</i> (Müller 1774)	336	418
	7.) <i>Lymnaea (Galba) glabra</i> (Müller 1774)	336	358
	8.) <i>Lymnaea (Galba) palustris</i> (Müller 1774)	336	384
	<i>Lymnaea (Lymnaea) stagnalis</i> (Linnaeus 1758)	336	410
	<i>Lymnaea (Radix) auricularia</i> (Linnaeus 1758)	336	333
	<i>Lymnaea (Radix) peregra</i> (Müller 1774)	336	389
	<i>Myxas glutinosa</i> (Müller 1774)		
Planorbidae	<i>Planorbis planorbis</i> (Linnaeus 1758)	335	311
	<i>Planorbis carinatus</i> Müller 1774	336	336
	9.) <i>Anisus (Anisus) leucostoma</i> (Millet 1813)		
	(? = <i>Planorbis spirorbis</i> (Linnaeus))		
	<i>Anisus (Disculifer) vortex</i> (Linnaeus 1758)	336	424
	<i>Anisus (Disculifer) vorticalus</i> (Troschel 1834)	336	425
	<i>Bathyomphalus contortus</i> (Linnaeus 1758)	336	340
	<i>Gyraulus laevis</i> (Alder 1838)	336	366
	<i>Gyraulus acronicus</i> (Férussac 1807)		
	<i>Gyraulus albus</i> (Müller 1774)	336	325
	<i>Armiger crista</i> (Linnaeus 1758)	336	343
	<i>Hippeutis complanatus</i> (Linnaeus 1758)	336	339
	<i>Segmentina nitida</i> (Müller 1774)	335	320
	<i>Planorbarius corneus</i> (Linnaeus 1758)	336	341
	<i>Menetus (Micromenetus) dilatatus</i> (Gould 1841)	336	347
Ancylidae	<i>Ancylus fluviatilis</i> Müller 1774	363	502
Acroloxidae	<i>Acroloxus lacustris</i> (Linnaeus 1758)	363	503
Bivalvia			
Margaritiferidae	<i>Margaritifera margaritifera</i> (Linnaeus 1758)	495	1456
Unionidae	<i>Unio pictorum</i> (Linnaeus 1758)	495	1455
	<i>Unio tumidus</i> Philipsson 1788	336	444
	<i>Anodonta cygnea</i> (Linnaeus 1758)	336	429
	10.) <i>Anodonta anatina</i> (Linnaeus 1758)	336	426
	<i>Pseudanodonta complanata</i> (Rossmässler 1835)		
	(= <i>Anodonta minima</i> auctt, non Millet)		
Sphaeriidae	<i>Sphaerium (Sphaerium) corneum</i> (Linnaeus 1758)	336	427
	<i>Sphaerium (Sphaeriastrum) rivicola</i> (Lamarck 1818)	336	438
	<i>Sphaerium (Cyrenastrum) solidum</i> (Normand 1844)	336	439
	<i>Sphaerium (Musculium) transversum</i> (Say 1829)	336	443
	<i>Sphaerium (Musculium) lacustre</i> (Müller 1774)	336	431
	11.) <i>Pisidium amnicum</i> (Müller 1774)	335	290
	<i>Pisidium casertanum</i> (Poli 1791)	587	1713
	<i>Pisidium conventus</i> Clessin 1877		
	<i>Pisidium personatum</i> Malm 1855		
	<i>Pisidium obtusale</i> (Lamarck 1818)	336	436
	<i>Pisidium milium</i> Held 1836	336	433
	12.) <i>Pisidium pseudosphaerium</i> Schlesch 1947		

	<i>Pisidium subtruncatum</i> Malm 1855	336	440
	<i>Pisidium supinum</i> A. Schmidt 1851	336	441
	<i>Pisidium henslowanum</i> (Sheppard 1823)	336	430
	<i>Pisidium lilljeborgii</i> Clessin 1886		
	<i>Pisidium hibernicum</i> Westerlund 1894		
	<i>Pisidium nitidum</i> Jenyns 1832	336	435
	<i>Pisidium pulchellum</i> Jenyns 1832	336	437
	<i>Pisidium moitessierianum</i> Paladilhe 1866	336	434
	<i>Pisidium tenuilineatum</i> Stelfox 1918	336	442
Dreissenidae	<i>Dreissena polymorpha</i> (Pallas 1771)	351	484

NOTES

- 1.) *Valvata pulchella* Studer 1820 of some authors, but others regard this name as a *nomen nudum*. Sometimes placed in the subgenus *Atropidina* Lindholm.
- 2.) *Hydrobia stagnalis* (Baster 1765) or *H. stagnorum* (Gmelin 1790) of some continental authors (*Basteria*, **9** (1945): 66).
- 3.) The form *denticulata* Montagu is sometimes regarded as a separate species.
- 4.) *Leucophytia* is regarded by Zilch (*Handbuch der Paläozoologie*, **6**: 75) as a subgenus of *Auriculinella* Tausch.
- 5.) There is still much uncertainty about the species of *Physa* present in the British Isles apart from *P. fontinalis*. *P. acuta* is fairly well characterized. It is not uncommon in rivers and canals in England and in view of its wide European distribution is possibly indigenous. Our remaining species are probably introductions from north America. *P. gyrina* occurs in south Wales (*Glamorgan Nat. Trust ann. Bull.* **13** (1974): 15). *P. heterostropha* has often been reported, but the records need confirmation and more than one species has probably been confused under this name. Further species have been reported from greenhouses (*J. Conch.*, *Lond.* **23**: 181; *British Snails* (1969): 274). For an excellent illustrated key to the Physidae of New York State, see Search (*Cornell Univ. agric. exper. Station, Ithaca*), **1** (1971), no. 4.
- 6.) Relationships within the Lymnaeidae remain unclear, and I have therefore followed the advice of Dr. Hubendick in retaining most of our forms within the genus *Lymnaea*.
- 7.) Alternatively placed in the subgenus *Leptolimnea* Swainson (*Omphiscola* Beck, non Rafinesque).
- 8.) Alternatively placed in the subgenus *Stagnicola* Jeffreys.
- 9.) Whatever the original identity of Linné's *Helix spirorbis* may have been, the broadly-coiled form traditionally known as *spirorbis* may possibly be a species distinct from *leucostoma*. It occurs in Britain, though it is less common than typical narrowly-coiled *leucostoma*. In Sweden—presumably the source of Linné's material—only *spirorbis* is known to occur (information from Dr. Hubendick).
- 10.) The continued use of this name in the commonly accepted sense remains *sub judice* (*Bull. zool. Nomencl.*, **21**: 432; **22**: 213; *J. Conch.*, *Lond.* **26**: 251). The name *piscinalis* Nilsson, 1823 is used by some continental authors, especially in Scandinavia.
- 11.) Subgenera in northern hemisphere *Pisidium* are not satisfactorily delimited and have therefore been omitted.
- 12.) For the authorship of this species see *J. Conch.*, *Lond.* **26**: 258.

CHARONIA LAMPAS (L) (GASTROPODA: CYMATIIDAE) LIVING OFF THE CORNISH COAST

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'Shang-ri La', Reskadinnick, Camborne, Cornwall

(Read before the Society, 15 November 1975)

Abstract: This paper records a living specimen of *Charonia lampas* (L.), taken in *c.* 80 m., 5-6 miles S.E. of Wolf Rock off the Cornish coast, and lists all known British reports of the species.

A living example of *Charonia lampas* (L.), measuring 200 mm \times 100 mm, was brought ashore by the Newlyn Trawler *Karen*, skipper Mr. L. Lashbrook, on 21 March 1975. The trawler had been working in *c.* 80 m at approximately 49° 52' N 5° 42' W (5-6 miles S.E. of Wolf Rock in Sea Area 18) between 18 and 21 March. Little seems to be known about the ecology of this species. Brehaut (1973) suggests that it may feed on scallops in the Channel Isles, and certainly scallops were taken in the trawl off the Wolf Rock on the present occasion. However Nordsieck (1968, p. 110) writes of its predilection for starfish, and states that in winter it occurs on mud. Like the Sarnian specimen figured by Crowley (1961), this Cornish example has an eroded spire and is encrusted with marine growths, including the bryozoans *Microporella ciliata* (Pallas) and *Hippopodinella lata* (Busk) (= *Lepralia adpressa*): it was the presence on one of Jeffreys' specimens of '*Lepralia coccinea*', said to occur only as far south as the British Isles, that convinced him that *Charonia* had indeed been taken alive in the vicinity of the Channel Isles, and not further south, as disbelieving critics averred. Skipper Lashbrook states that empty shells of the triton have been taken by his vessel previously, but this is the first live one that he has seen.

The following records appear to encompass all those hitherto known from the Conchological Society's Marine Census Area.

Channel Isles (Sea Area 17). 1825-1847. Three or four living specimens (Jeffreys, 1865 4, p. 302; Crowley, 1961).

Ditto. 1972. Three living specimens, one of which was from Hurd Deep, north of the Isles (Brehaut, 1972).

Fastnet (Sea Area 37). 1970-1971. Four living specimens off the coast of Co. Kerry (O'Riordan, 1972).

That such a conspicuous species has not been reported for over a hundred years until these recent discoveries, could reflect the growing interest in the distribution of marine fauna, or possibly that this species is extending its range northwards. If the latter were true, it would be against the tendency for many 'southern' species to become rarer as a result of lower sea temperatures in the Western Channel (Southward, 1967; Southward and Butler, 1972), although one might expect any climatic effects to be more obvious near the shore.

I thank Mr. P. Pearman who recognized this as a rare species in British waters when it was brought to Messrs. Harveys, Fish Merchants, by Mr. Lashbrook; Mr. A. Crocker who kept it alive in his aquarium; and Mr. G. H. Buchanan-Wollaston, Fishery Officer, Newlyn for providing all the data. I am also indebted to Dr. A. R. D. Stebbing for identifying the bryozoans. The specimen is now in the spirit collection of the Marine Biological Association's Museum at Plymouth.

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SECONDARY BROODING OF TEMPORARY
DWARF MALES IN *EPHIPPODONTA*
(*EPHIPPODONTINA*) *OEDIPUS*
SP. NOV. (BIVALVIA: LEPTONACEA)

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(Read before the Society, 15 November 1975)

Abstract: *Ephippodonta* (*Ephippodontina*) *oedipus* n.sp. is the second species of the sub-genus and the fifth species of the genus to be described. It is commensal with a nestling series of associated invertebrates in the galleries of living and dead sublittoral coral heads.

The shell is dorso-ventrally flattened and covered by the reflected middle mantle fold. Pallial papillae on the mantle protect the animal. The young are incubated in the ctenidial marsupium of the female, but two sexually mature juveniles thought to be dwarf males are further incubated in a pair of pallial pouches. They are attached by a byssus to the periostracum of the female. In this position they probably fertilize the female.

The major trends within the Galeommatidae show an advance towards commensalism and progressive degrees of specialization are apparent.

The Leptonacea Gray (=Erycinacea Fischer) comprise a fascinating assemblage of bivalve molluscs that have been little studied. Where a study has been made, however, they have revealed a diversity of morphological adaptations that is rarely seen elsewhere within the Bivalvia.

Amongst the superfamily as a whole a number of trends are apparent mainly stemming from an advance towards symbiosis (a term used here in the widest possible sense) for many leptonaceans live in association with other, typically intertidal, animals. There is a reduction both in size and thickness of the shell and a reduction in the number and size of the hinge teeth. Associated with these trends is a tendency to rely, more and more, upon the reflected middle fold of the mantle for protection. The acquisition of a more sophisticated pattern of breeding together with the subsequent protection of the developing young into late larval life in a ctenidial marsupium were prerequisites for the successful adoption of a commensal habit. Such modifications can be allied to the neotenus retention of the larval byssus by the adult—possibly indicating that the Leptonacea are paedomorphic.

Nowhere are these trends more clearly demonstrated than in the Galeommatidae Gray, one of five families recognized by Chavan (1969). This paper concerns itself with a new species of galeommatid, *Ephippodonta* (*Ephippodontina*) *oedipus*, which possesses a number of interesting eccentricities. Only one species of the sub-genus, namely *E. (Ephippodontina) murakamii* (Kuroda, 1945), has hitherto been described. This study therefore provides further data pertinent to our understanding of a little known group of bivalves.

Galeommatidae Gray

The Galeommatidae contain some 27 genera (Chavan, 1969) which, with only a few exceptions, e.g. *Galeomma* (Popham, 1940; B. S. Morton, 1973, 1975), *Phlyctaenachlamys* (Popham, 1939), *Divariscintilla* (Judd, 1971), *Scintilla* (Arakawa, 1960b, 1961), *Scintillona* (J. E. Morton, 1957), *Achasmea* (Habe, 1962), are inadequately described.

Table 1 summarizes the available ecological data which show that the Galeommatidae range in life style from free living species (e.g. *Galeomma turtoni*, *Scintilla vitrea* and *S. violescens*) to clearly defined commensals specifically inhabiting the burrows of a number of intertidal crustaceans (e.g. *Divariscintilla maoria*, *Phlyctaenachlamys lysiosquillina*, *Ehippodonta macdougalli*, *E. lunata* and *E. turnbullae*), echiuroids (e.g. *Achasmea thalassemicola*) and holothurians (e.g. *Scintillona zelandica*). The association of some species with other organisms (e.g. *Galeomma polita*, *G. (Paralepida) takii*) is less easy to define.

TABLE 1
The Galeommatidae—habitats and hosts

	HOST OR HABITAT	REFERENCE SOURCE
<i>Scintilla vitrea</i>	Free living	Arakawa, 1960b
<i>Scintilla violescens</i>	Free living	Arakawa, 1961
<i>Scintillona zelandica</i>	<i>Trochodota dendyi</i>	J. E. Morton, 1957
<i>Galeomma turtoni</i>	Free living	Popham, 1940
<i>Galeomma (Paralepida) takii</i>	Intertidal, under stones: loosely associated with nestling invertebrates, e.g. <i>Alpheus</i> sp. <i>Harmothoe</i> sp.	B. S. Morton, 1973
<i>Galeomma polita</i>		B. S. Morton, 1975
<i>Thyreopsis coralliophila</i> = <i>Galeomma</i> sp. (Franc, 1960)	Coral	Adams, 1868
<i>Libratula plana</i>	Coral	Pease, 1865
<i>Ehippodonta murakamii</i>	<i>Dendrophylla cribosa</i>	Kuroda, 1945
		Arakawa, 1960a
<i>Ehippodonta macdougalli</i>	<i>Axius plectorhynchus</i>	Tate, 1889
<i>Ehippodonta lunata</i>		Buick & Bowden, 1951
<i>Ehippodonta turnbullae</i>		
<i>Divariscintilla maoria</i>	<i>Heterosquilla tricarinata</i>	Judd, 1971
<i>Phlyctaenachlamys lysiosquillina</i>	<i>Lysiosquilla maculata</i>	Popham, 1939
<i>Achasmea thalassemicola</i>	<i>Thalassema mucosum</i>	Habe, 1962

Genus *Ehippodonta* Tate, 1889 (Fig. 4C)

Generic characteristics: Small shells (1–12 mm long), dorso-ventrally flattened, semi-elliptical in outline, but laterally angular. Shell anteriorly and posteriorly emarginated, externally striated, papillose or reticulate. Hinge margin straight. Ligament bounded on each side by obtuse tooth with bifid crown. The genus is divided into three subgenera.

E. (Ehippodonta) Tate, 1889

Type species: *E. (Ehippodonta) lunata* (Tate, 1889)

E. (Ehippodontina) Kuroda, 1945 (Fig. 4D)

Semi-elliptical in outline, not laterally angular. Shell anteriorly and posteriorly emarginated. The surface of the shell is finely reticulate. Hinge margin straight. The hinge is almost edentulous, there being no cardinals and only thickened, indistinct laterals.

Type species: *E. (Ehippodontina) murakamii* (Kuroda, 1945)

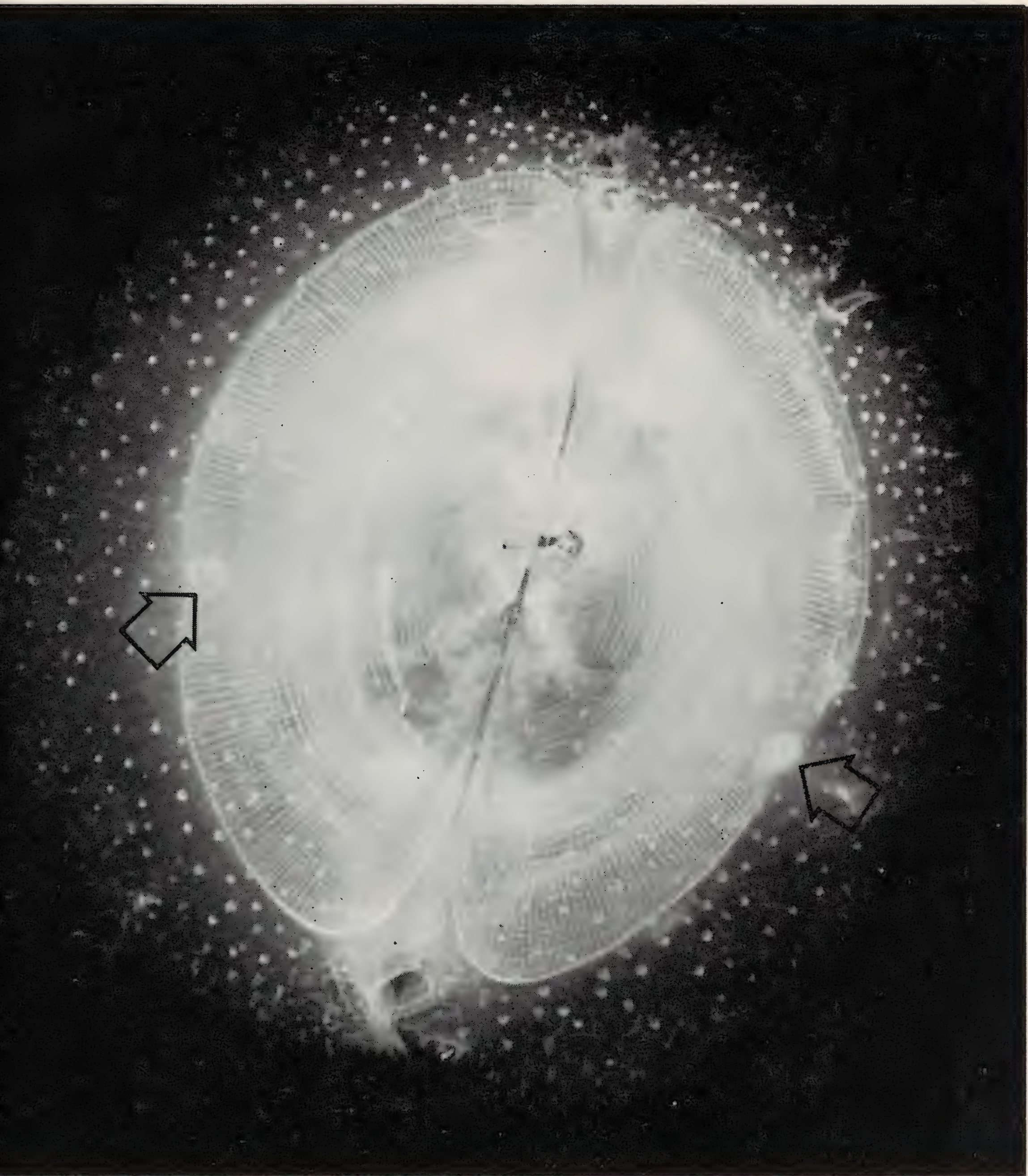
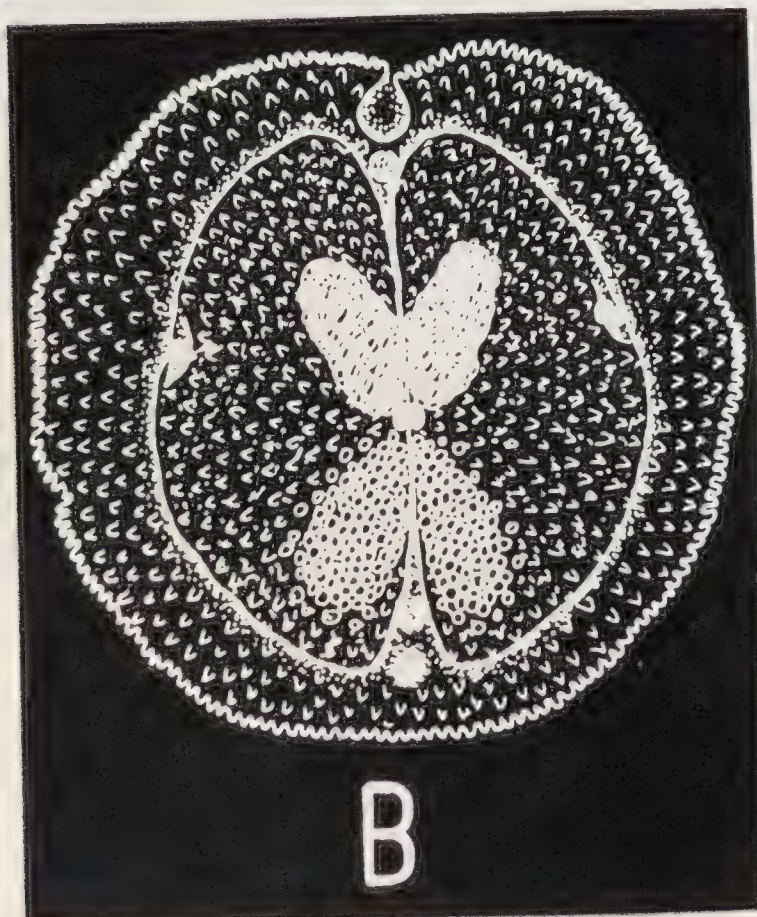
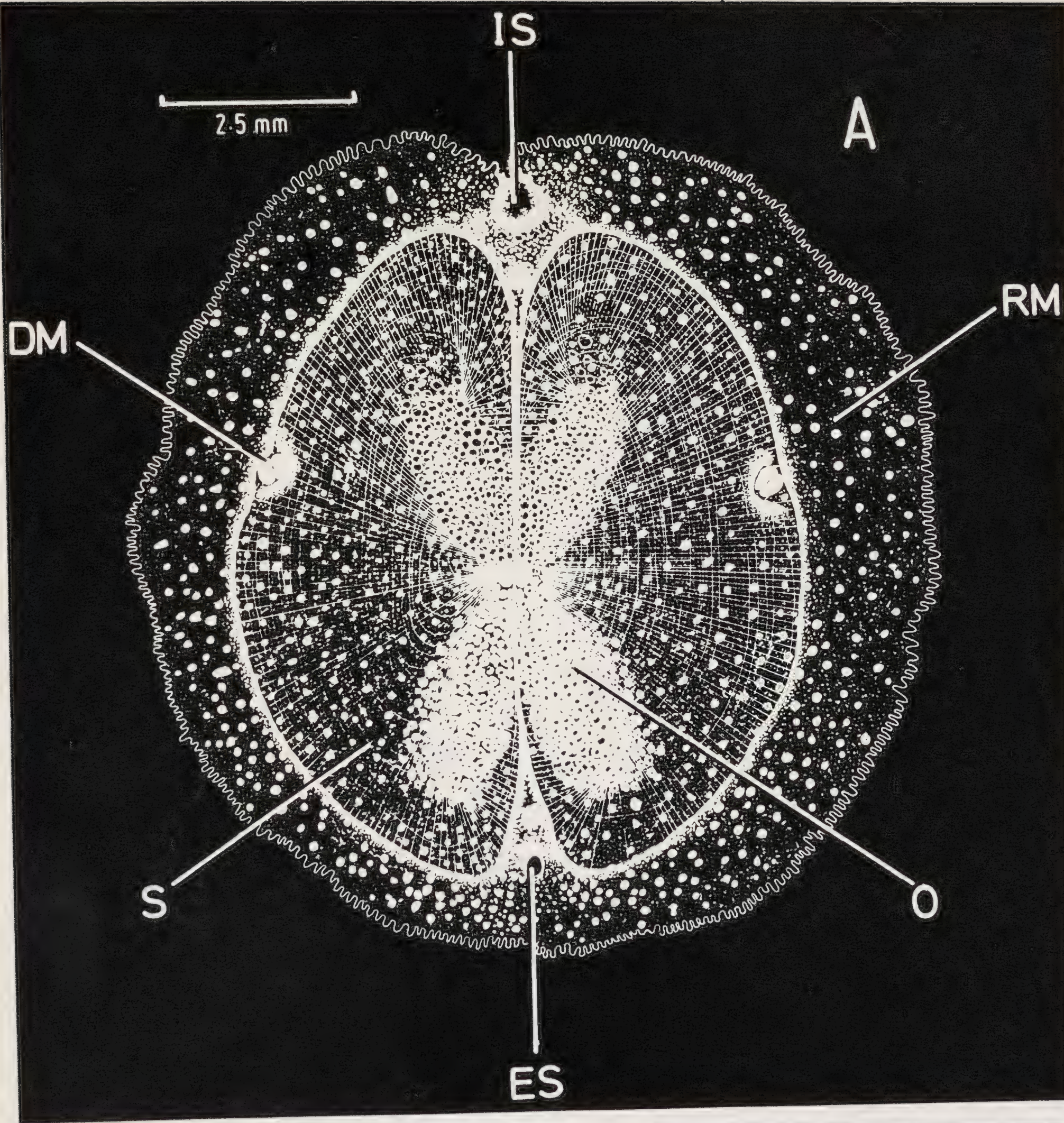


Plate 3. *Ehippodonta* (*Ehippodontina*) *oedipus* sp. nov. The living adult female. The dwarf males within their pouches are arrowed.



E. (Ephippodontoana) Habe, 1951 (Fig. 4E)

Almost completely circular in outline. Hinge margin diametral. Radial papillae cover the whole of the shell with radial riblets (costae) regularly indenting the shell margin ventrally.

Type species: *E. (Ephippodontoana) macdougalli* (Tate, 1889).

Ephippodonta (Ephippodontina) oedipus, sp. NOV.

Plate 3; Text figures 1-3, 4D, 5E)

Holotype: British Museum, Natural History (BMNH), London. 1975 42/1. Paratypes: BMNH. 1975 42/2. Australian Museum (AM), Sydney. c. 99127/1, 2 and 3.

Type locality: Sublittoral; 2-6 fathoms. West coast of Chek Chau Island, Mirs Bay, Hong Kong. Living within the galleries of coral heads, both living and dead, and associated (notably) with a pair of crustaceans (*Alpheus* sp.), a single ophiuroid (*Macrophiothrix* cf. *aspidota* Müller and Troschel) and other nestling associates.

TABLE 2
Shell dimensions (mm)

SPECIMEN	LENGTH	WIDTH
Holotype BMNH 1975 42/1	6.0	5.0
Paratype BMNH 1975 42/2	12.0	10.0*
Paratype AM c99127/1	6.4	2.4†
Paratype AM c99127/2	6.4	2.8†
Paratype AM c99127/3	6.3	2.8†

* measured with valves opened out horizontally, † measured with valves adducted.

ANATOMY AND MORPHOLOGY

The adult female. The shell of female specimens of *E. (Ephippodontina) oedipus* is fragile, white and almost translucent owing to its thinness. The valves are widely separated and held horizontally in life (Fig. 1A). The hinge margin is straight, but somewhat emarginated anteriorly and posteriorly. In transverse and longitudinal section, the shell of *E. (Ephippodontina) oedipus* is much flatter than that of *E. (Ephippodontina) murakamii*. The shell is smoothly and regularly semi-elliptical in outline. The prodissoconch is clearly visible. A puckering of the ventral margin of each valve of mature females occurs antero-laterally. This is caused by the presence of a temporary dwarf male (Plate 3), as will be explained later.

The sculpture of the shell of *E. (Ephippodontina) oedipus* comprises a fine and densely reticulate network of riblets or costae and concentric striae. At the intersections of striae and costae a small spine projects outwards from the shell. The ornament of the shell of *E. (Ephippodontoana)* on the other hand comprises extremely fine and dense radiating dichotomously branching costae, as in *Galeomma turtoni* (Popham, 1940), set with minute granulae in a concentric arrangement all over the valve (Odhner, 1917). The shell of *E. (Ephippodontina) oedipus* possesses no cardinal hinge teeth and the lateral teeth (if representing modified teeth at all) comprise lateral thickenings of the dorsal margin of the shell. This feature closely allies the new species with the sub-genus *E. (Ephippodontina)* (Kuroda, 1945) and not with the superficially similar but toothed *E. (Ephippodontoana)* (Habe, 1951) and the genus *Galeomma* (B. S. Morton, 1973). I have examined an authenticated specimen of *E. (Ephippodontina) murakamii*, however, and in this species the

Fig. 1. (Opposite) *Ephippodonta (Ephippodontina) oedipus*. A Diagram of the living female viewed dorsally and with siphonal tentacles B withdrawn and C extended. DM dwarf male; ES exhalant siphon; IS inhalant siphon; O ovary; RM reflected mantle; S shell.

two lateral teeth are much larger. Arakawa (1960a) describes *E. (Ephippodonta) murakamii* as possessing a single cardinal tooth in each valve.

The dorso-ventral flattening of the shell of *E. (Ephippodonta) oedipus* represents one way by which a bivalve can attain a limpet-like mode of life. A small byssus anchors the flattened *E. (Ephippodonta) oedipus* to the coral surface. The thin, sculptured shell is overlain by the reflected middle fold of the mantle which also bears numerous papillae thought, as in *Divariscintilla maoria* (Judd, 1971), *Galeomma (Paralepida) takii* and *G. polita* (B. S. Morton, 1973, 1975) to be capable of autotomy and of releasing a noxious secretion to deter would-be predators. Like *G. polita*, *E. (Ephippodonta) oedipus* also possesses a somewhat smaller pair of eversible tentacles located above the exhalant and the inhalant siphons. These, when everted (Fig. 1C), serve a defensive function, possibly in dymanic display. Since the shell is thin and fragile, protection is provided by the mantle. Arakawa (1960a) describes *E. (Ephippodonta) murakamii* as not being covered by a reflected mantle.

Both demibranchs of each ctenidium are modified to form a marsupium as in a variety of other leptonaceans and in a number of galeommatids (B. S. Morton, 1973). This involves a reduction in the number of inter-lamellar junctions and an increase in the number of epithelial mucous cells. The young are probably released as D stage, planktotrophic larvae, as in *Scintilla vitrea* (Arakawa, 1960b).

A number of the larger individuals, ascertained by sectioning to be females, were found to possess either one, but more often two, small individuals of the same species contained within a pouch located on each side of the body. These are dwarf males (Fig. 2, DM).

The pouches (always two in number) never contained more than one small individual and were always developed in the reflected and enlarged middle fold of the mantle (MM) at the edge of the shell valves, somewhat anterior to the transverse mid line of the body. The presence of the dwarf males causes a distortion of the female shell in this region.

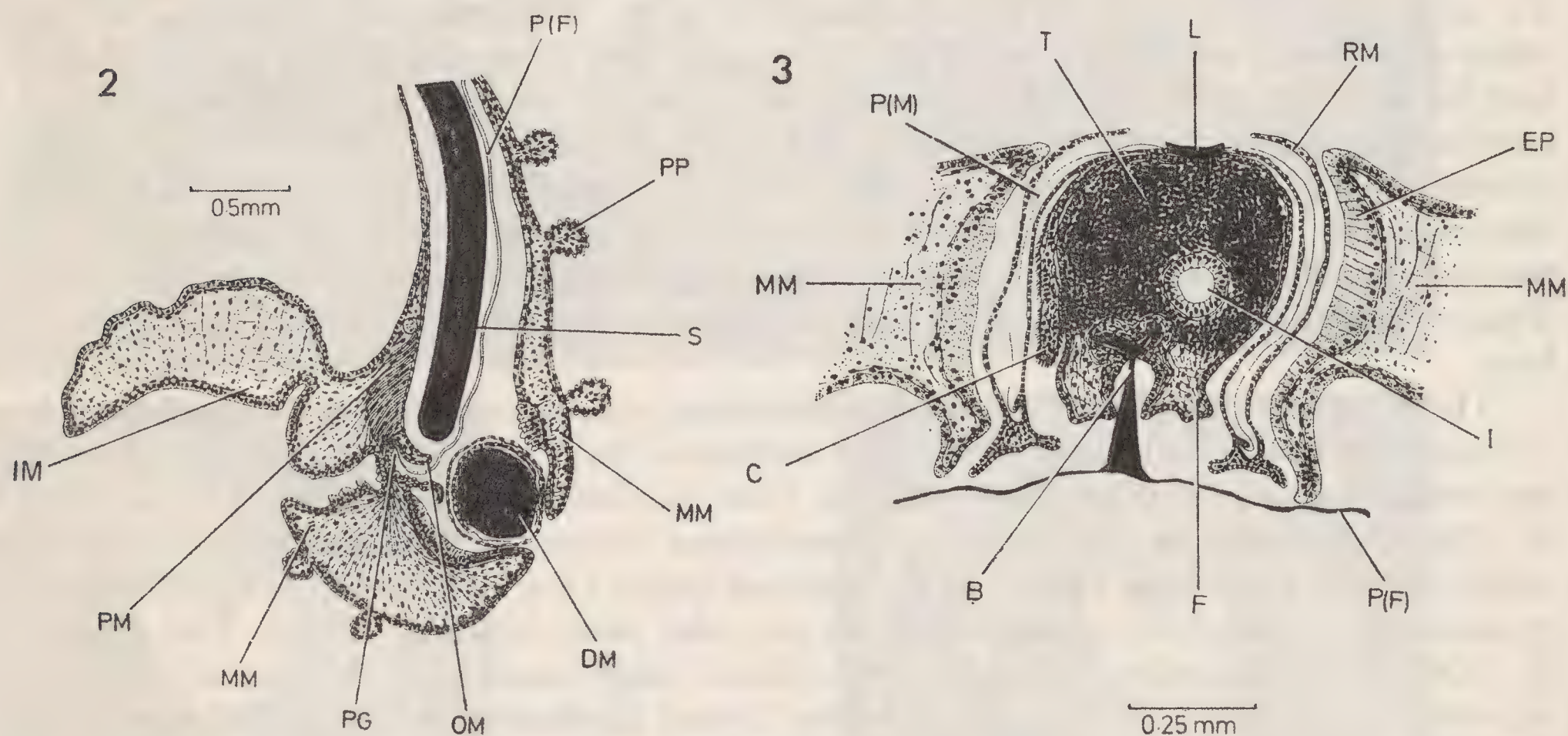


Fig. 2. *Ephippodonta (Ephippodonta) oedipus*. A section through the mantle margin of an adult female with a male located in the pallial pouch. DM dwarf male; IM inner mantle fold; MM middle mantle fold; OM outer mantle fold; P(F) periostracum of female; PG periostracal groove; PM pallial musculature; PP pallial papillae; S shell.

Fig. 3. *Ephippodonta (Ephippodonta) oedipus*. A section through the mantle of an adult female showing a dwarf male attached to the periostracum of the female by byssal threads. B byssus; C ctenidium; EP epithelium; F foot; I intestine; L ligament; MM middle mantle fold; P(F) periostracum of female; P(M) periostracum of male; RM reflected mantle; T testis.

The position of the pouches was constant for all adult females examined, but only larger, presumably mature females possessed dwarf males. Smaller specimens of *E. (Ephippodonta) oedipus*, i.e. approximately 4 mm in length or less, were found not to be mature and shown not to possess dwarf males.

The reflected middle mantle fold overlies the two layered periostracum (P(F)) secreted from within the periostracal groove (PG). The outer mantle (OM) fold is minute in comparison. The lining of the pouch is comprised of tall columnar cells, dissimilar to the flattened epithelia of other regions of the middle mantle fold. The dwarf males (Fig. 2, DM) were found to be attached by a byssus (B) to the periostracum (P(F)) of the female and to be closely enclosed by the surrounding protective pouch.

The male. The male (Fig. 3), no more than 1 mm in length, possesses a small shell, similarly covered by the reflected middle mantle fold. The gleaming prodissoconch is the most noticeable feature of the shell. Posteriorly the mantle fuses but is separate anteriorly as in the female. Only one of each pair of ctenidial demibranchs (C) was developed in the specimens sectioned; this representing an early phase in the normal development of a eulamellibranch bivalve, as in *Venericardia ventricosa* (Stasek, 1962). The digestive system (I) comprised, as in the female, a stomach, mid gut, rectum, style sac and digestive diverticula indicating that the male is able to collect and digest its own food. The foot (F) and byssal gland were well developed and a secretion from the latter secured purchase to the periostracum of the female (P(F)).

The most remarkable aspect of the dwarf male is the testis which was extensively developed and contained mature spermatozoa.

The mantle lobes of the female are free anteriorly forming a combined inhalant and pedal aperture. Posteriorly the inner mantle folds fuse; this being type A fusion (Yonge, 1957). The dwarf males are located close to the postero-ventral extremity of the inhalant/pedal aperture. Sperm released by the male would thus be taken into the mantle cavity of the female with the inhalant flow. The sperm would fertilize eggs contained within the ctenidial marsupia of the female.

Each discrete coral head, with its complement of specimens of *E. (Ephippodonta) oedipus* could well constitute a breeding colony, with little and only spasmodic genetic interchange occurring between colonies. It could well be therefore, as suggested earlier for *Galeomma takii* (B. S. Morton, 1973) that the dwarf males are, as the specific name suggests, progeny of the bigger female.

The disadvantages of such a relationship, in genetic terms, are possibly outweighed by the survival value afforded by this means of reproduction. The overriding incidence of protandry within the Leptonacea suggests that such dwarf males are only temporarily so and subsequently mature, with sex reversal, into females. This has yet to be proven, however.

BIOLOGY

Hitherto, the sub-genus *E. (Ephippodonta)* has been regarded as being monotypic; the only other species *E. (Ephippodonta) murakamii* being recorded from sublittoral coral heads (Kuroda, 1945; Arakawa, 1960a). The specimens of *E. (Ephippodonta) oedipus* from Hong Kong waters were similarly found within the internal galleries of living and dead coral heads, located at a depth of some 2–6 fathoms. Coral most commonly found to possess the commensals were *Acropora tumida*, *Goniopora lobata* and *Alveopora mortensenii*.

Typically 2 or 3, but on one occasion as many as 12 specimens of *E. (Ephippodonta) oedipus* have been found together and appear to share their niche with a number of other invertebrates of which a single ophiuroid *Macrophiothrix*, cf. *aspidota*, Müller and Troschel

and a pair of alpheids (*Alpheus* sp.) were commonly present. Another pair of alpheids (*A. malleodigitus*) were also occasionally found. Other associates included a scale worm (*Harmothoe*) and a variety of decapod and anomuran crustaceans, e.g. *Pilodius granulatus*, *Petrolisthes boscii*, *Pachycheles sculptus*. Significantly two other galeommatids, *G. (Paralepida) takii* and *G. polita* (B. S. Morton, 1973, 1975) have been shown to have a similar though looser relationship with a group of other invertebrates occupying another niche rarely investigated; that of large stones lying on firm intertidal muds. An alpheid was, possibly significantly, also a member of this community.

E. (Ehippodontina) oedipus lies with the shell valves extended horizontally closely applied to the galleries of the coral and gains protection from its secluded habit. The horizontally flattened shape, attached by a byssus, prevents dislodgement. It possibly capitalizes upon the respiratory currents of its nestling associates, particularly the alpheids, which bring oxygen and food material into the gallery.

DISCUSSION

The living members of the Galeommatidae, particularly the genera *Scintilla*, *Galeomma* and *Ehippodonta*, are interesting for the trends they demonstrate. Scintillids, e.g. *Divariscintilla maoria* (Judd, 1971) and *Scintilla vitrea* (Arakawa, 1960b) possess rounded shell valves, without a long straight hinge margin (Fig. 4A). The shell valves can be closely opposed in life. Members of the genus *Galeomma* (Fig. 4B) on the other hand possess semi-elliptical shell valves usually held at an angle of 45° to each other and are incapable of being completely opposed. The hinge margin of these species is straight. The hinge margin of the sub-genus *E. (Ehippodonta)* (Fig. 4C) is longer than that of *Galeomma*, but the shell margins are angular. *E. (Ehippodontina) oedipus* has an even longer hinge margin and the

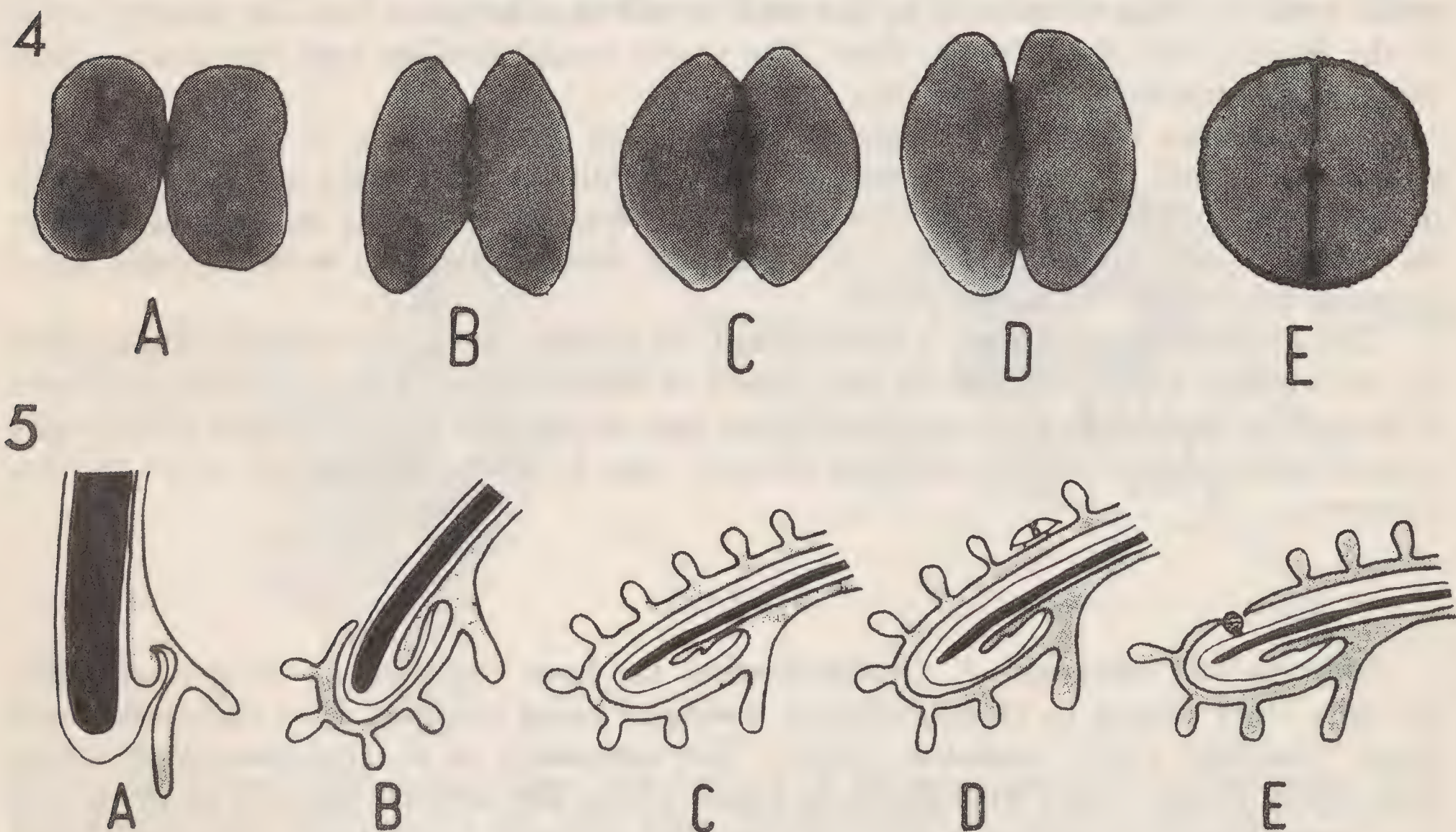


Fig. 4. The shell outlines of A *Scintilla*; B *Galeomma*; C *Ehippodonta* (*Ehippodonta*); D *Ehippodonta* (*Ehippodontina*); E *Ehippodonta* (*Ehippodontoana*).

Fig. 5. The mantle margin of A a typical bivalve; B *Scintilla*; C *Galeomma polita*; D *Galeomma* (*Paralepida*) *takii*; E *Ehippodonta* (*Ehippodontina*) *oedipus*.

shell valves, when opened out horizontally as they are in life, almost form a circle apart from a slight anterior and posterior emargination. The valves can only come together to an angle of some 110° . In *E. (Ephippodontoana)* the hinge margin is straight along its entire length and the shell valves are completely circular. Associated with this trend, one can also see a gradual reduction in the size and number of the hinge teeth and in the thickness of the shell itself. More importantly, however, this trend is also accompanied by a relative growth in importance of the mantle which comes progressively to cover the shell almost completely. Only the middle mantle fold is involved and this fold, primitively regarded as being sensory in the Bivalvia (Yonge, 1957), also tends to develop pallial papillae that can autotomize and, it is thought, release a noxious chemical (Judd, 1971; B. S. Morton, 1973, 1975). This deters the many small associates characteristically living with these species. Some, however, e.g. *Galeomma polita* and *E. (Ephippodontina) oedipus* possesses a pair of eversible tentacles, probably derived from smaller non-eversible tentacles seen in free living scintillids, e.g. *Scintilla vitrea* (Arakawa, 1960b), that serve, in dymanic display, to deter larger more persistent attackers.

Thus the effective protection of the animal has progressively shifted from the shell to the mantle. This trend follows that described above and in Fig. 5 the condition seen in a typical bivalve with the mantle protected by the shell is compared with the situation seen in *Scintilla* (Fig. 5B), *Galeomma polita* (Fig. 5C) and in *G. (Paralepida) takii* (Fig. 5D) where juveniles were found apparently to be gaining some degree of protection from the papillae of the mantle. *E. (Ephippodontina) oedipus* (Fig. 5E) represents a successive stage in this process where a pair of dwarf males have been found to inhabit pouches in the reflected mantle of adult females. These are thought to be temporary dwarf males.

Among the Mollusca separate sexes are most often considered to be primitive (Purchon, 1968) and it is usually held that hermaphroditism is secondarily derived from a gonochoristic condition. This may not necessarily be true since, as pointed out by Fretter and Graham (1964), there is some evidence for regarding the hermaphroditic state as a primitive one, particularly in the phylum Mollusca.

Hermaphroditism is most often recognized in those members of the Bivalvia occupying habitats where they are less likely to meet with other members of the same species. Thus sedentary, freshwater and commensal and parasitic bivalves are typically, and more often, protogynous or protandric consecutive hermaphrodites. Pelseneer (1895, 1911) first noted that many hermaphrodites also incubate their eggs and developing larvae, often within a ctenidial marsupium, i.e. within the suprabranchial chamber.

Other bivalves protect juveniles within the infrabranchial chamber, e.g. *Pseudopythina subsinuata* (B. S. Morton, 1972) where the young, initially incubated within the suprabranchial chamber, are released, and subsequently attach to the byssus of a much larger female. They become temporary 'dwarf males' and eventually fertilize the female host. Species of *Cardita*, e.g. *C. carpenteri* (Yonge, 1969), incubate their young within the ctenidium and subsequently brood them secondarily in a brood pouch in the shell.

In *Galeomma takii* a similar situation is seen in that young are incubated within a ctenidial marsupium, but newly released young were also seen crawling over the back of an adult female (B. S. Morton, 1973) deriving, it was suspected, some protection from the pallial tentacles of the female. The condition seen in *E. (Ephippodontina) oedipus* is as advanced as any yet described for the Leptonacea though an apparent parallelism exists within the Montacutidae. Dwarf males are found in *Montacuta phaseolinis* (Deroux, 1960) and *M. floridiana* and *M. percompressa* (Jenner and McCrary, 1968) where males of both species are retained within the mantle tissue of the female; the male of the latter species being reduced to a spherical mass of gonadal tissues. The dwarf male of the parasitic *Entovalva* is also housed within the mantle of the female. Such species have not been studied in detail, however. It would seem probable, judging by the fact that the dwarf

males of *E. (Ephippodonta) oedipus* possess a full complement of digestive organs and at least one demibranch in the mantle cavity, that they are so only temporarily and that they ultimately, as in the greater majority of the Leptonacea, undergo sex reversal. Such a mechanism is important in demonstrating one way in which true, permanent, dwarf males might have evolved in the dioecious parasitic *Entovalva*. More importantly, however, it is a mechanism for survival that is irrevocably bound up with the trend in the Galeommatidae towards commensalism (see Table 1). Thus the relatively unspecialized scintillids, with rounded opposing shell valves, are free-living (Arakawa, 1960b, 1961), whereas species of *Galeomma* (B. S. Morton, 1973, 1975) are loosely associated with a fauna typically inhabiting the undersurface of stones, located on a sandy or muddy substrate. Significantly an alpheid shrimp is a prominent member of this community. *E. (Ephippodonta) oedipus* and *E. (Ephippodonta) murakamii* (Kuroda, 1945; Arakawa, 1960a) occur in the galleries of coral heads associated with a well defined and closely knit community of which an alpheid is again a prominent member. The possibly final step in this trend is the close association, probably commensal, between some three species of *E. (Ephippodonta)* and the burrowing crustacean *Axius plectorhynchus* (Buick and Bowden, 1951). This association warrants further study especially with regard to the reproductive adaptation of the commensals. *E. (Ephippodonta) oedipus* is quite distinct from *E. (Ephippodonta) murakamii*, a shell of which I have examined. The observations of Arakawa (1960a) upon the ecology of *E. (Ephippodonta) murakamii* similarly closely ally the two obviously related species—both living within coral heads.

The suggestion by Arakawa (1960a) that *E. (Ephippodonta) murakamii* possess only a single (cardinal) tooth in each valve is clearly erroneous as, it is suspected, is the suggestion that the shell is not covered by the mantle. The alternative is that Arakawa (1960a) had collected a third, hitherto undescribed, galeommatid also possibly belonging to the genus *Ephippodonta*.

ACKNOWLEDGEMENTS

I am grateful to Dr. R. G. Wear of the Marine Sciences Laboratory, The Chinese University of Hong Kong for boat facilities provided during this study and to Hugh Richards and Tom Watson who kindly collected the coral heads in which *E. (Ephippodonta) oedipus* was found. I am also grateful for the help and advice of Dr. John Taylor and Mrs. S. Whybrow of the British Museum (Natural History), Dr. R. Manning of the Smithsonian Institution for identifying the crustaceans and to Dr. T. Habe of the National Science Museum for the loan of an authenticated specimen of *E. (Ephippodonta) murakamii*, and to Dr. D. M. Devaney of the Bishop Museum for identifying *Macrophiothrix* cf. *aspidota*.

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TYPE SPECIMENS IN THE JANE SAUL COLLECTION, UNIVERSITY MUSEUM OF ZOOLOGY, CAMBRIDGE

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(Read before the Society, 17 May 1975)

Abstract: A list of all known type specimens in the collection of Jane Saul, Cambridge University Museum of Zoology, is presented, together with information on their present status, measurements and localities. The holotypes of *Cypraea venusta* Sowerby 1847 and *Voluta becki* Broderip 1836 are figured for the first time.

Jane Saul's collection of shells (an estimated 20,000) was received by the University Museum of Zoology, Cambridge in 1895. The shells were laid loose on cotton wool in the original cabinets. Miss Saul (1807-1895), of Limehouse in London, acquired her shells from dealers and there is no evidence that she ever collected material in the field. The collection must be viewed in the context of the times in which she lived, but even so the standard of labelling was poor. Many of the specimens were unlabelled and almost all the material was unlocalized, the majority of labels consisting solely of a species name. It has sometimes been possible to infer provenance when a specimen can be identified with an original description or figure. Further details of the previous history of the collection are given by Dance (1966) and Kay (1968).

The Saul collection is renowned for its content of rarities, particularly of *Cypraea*, *Conus* and *Murex*. The collection contains type material and many specimens figured in the monographs of Reeve and Sowerby (1843-78) and Sowerby (1842-87). The specimens of nomenclatural importance were not labelled as such by the original authors, and the main task has been to identify types in the collection by comparison with the original descriptions and plates. We are already aware of eight authors who based their descriptions of new species on material now contained in the Saul collection, and there is unfortunately no way at present of ensuring that all the types have been identified.

TYPE SPECIMENS

The following list of type material includes specimens which have been identified in the Saul collection, and specimens which are cited in the literature as being contained in the collection but which have not been traced. Holotypes are recognized as such only where the original description states clearly that the species was based on a single specimen. Other types are accepted as syntypes, or lectotypes where designated by previous workers.

No lectotypes are selected here. The form of the entries is as follows: genus and species of the type description together with author and date of publication for nomenclatural purposes and reference to the original description; status of the specimen in nomenclature; reference to a figure of the specimen; measurements made on the identified specimen (for gastropods the measurements are height, and maximum and minimum diameter as defined by Cox (1960) except for Cypraeidae where the measurements are length, diameter and height; for bivalves the measurements are length, height and maximum width); locality (usually as cited in the original description); other points. All material consists of shells only and gastropods have been cleaned so that no radula or operculum remains. There exists a small manuscript notebook with entries of *Cypraea*, *Murex*, *Conus* and *Haliotis*, referred to in the text as the Saul catalogue.

GASTROPODA

Cypraea acutidentata Gaskoin, 1836. (Gaskoin, 1835). Holotype. The holotype was broken by Gaskoin, and only 8 fragments remain. Sowerby (1870) stated 'The original type was broken by Mr. Gaskoin after description, and the fragments preserved in Miss Saul's collection are quite incomplete'. Isle of Muerte, Bay of Guayaquil, Ecuador.

Cypraea barclayi Reeve, 1857. Holotype, first figured by Reeve (1857, pl. 38, fig. 4a, b). Further details of types of *Cypraea* and *Luponia* are given by Kay (1968).

Cypraea modesta Sowerby, 1870. Holotype.

Cypraea saulae Gaskoin, 1843. Holotype.

Cypraea trizonata Sowerby, 1870. Holotype.

Cypraea venusta Sowerby, 1847. Holotype. The holotype does not appear to have been figured previously and is illustrated in Plate 4. Length 71 mm, diameter 43 mm, height 37.5 mm. Port Adelaide, South Australia. The shell was referred to by G. B. Sowerby II (1870, species 57, as *C. thatcheri* Cox) who overlooked the valid publication of the name *venusta* by his father.

Helix filicosta Pfeiffer, 1845. A specimen from the Saul collection was figured by Reeve (1851-54, pl. 204, fig. 1437). Not located.

Helix rhombostoma Pfeiffer, 1845. This species was based on specimens in the Saul and Metcalf collections. Not located.

Helix sauliae Pfeiffer, 1845. This species was based on specimens in the Cuming and Saul collections. Not located.

Luponia castanea Higgins, 1868. Holotype figured by Higgins (1868, pl. 14, fig. 1, 1a, 1b) and Sowerby (1870, pl. 29, fig. 302, 303).

Murex ambiguus Reeve, 1845. (Reeve, 1845-46). The holotype is the specimen figured by Reeve (1845-46, pl. 13, fig. 51). Not located, although there is an entry (as No. 114) in the Saul catalogue. Locality unknown. The species was originally described by Reeve (1845a).

Murex crassivaricosa Reeve, 1845. (Reeve, 1845-46). Holotype, the specimen figured by Reeve (1845-46, pl. 9, fig. 33). Height 61 mm, diameters 40, 31 mm. Locality unknown. The specimen has a Saul label 'Crassivaricosa' and Saul Cat. No. 111. The species was originally described by Reeve (1845a).

Murex laqueatus Sowerby, 1841. (Sowerby, 1840). Holotype, figured by Sowerby (1832-41, *Murex* species 45, fig. 78), and Reeve (1845-46, pl. 26, fig. 115). Height 31 mm, diameters 19, 16 mm. Locality unknown. Saul Cat. No. 39.

Murex nigrispinosus Reeve, 1845. (Reeve, 1845-46). Holotype, figured by Reeve (1845-46, pl. 20, fig. 79). Height 92 mm. Locality unknown. The specimen has a Saul label 'Nigrispinosus' and Saul Cat. No. 119. The species was originally described by Reeve (1845a).

Murex osseus Reeve, 1845. (Reeve, 1845–46). Holotype, figured by Reeve (1845–46, pl. 14, fig. 60). Height 74 mm, diameters 40, 28 mm. Locality unknown. The specimen has a Saul label 'Osseus' and Saul Cat. No. 117. The species was originally described by Reeve (1845a).

Murex rusticus Reeve, 1845. (Reeve, 1845–46). The holotype was figured by Reeve (1845–46, pl. 33, fig. 163). Not located, although there is an entry (as No. 141) in the Saul catalogue. Locality unknown. The species was originally described by Reeve (1845b).

Murex saulii Sowerby, 1841. (Sowerby, 1840). Syntype. In the original description of this species Sowerby stated 'H. Cuming legit. Mus. Saul, Stainforth, Reeves'. The specimen figured by Sowerby (1832–41, species 34, fig. 77) was from the Cuming collection. The specimen figured by Reeve (1845–46, pl. 8, fig. 31) is in the Saul collection. Saul Cat. No. 30.

Murex scabrosus Sowerby, 1841. (Sowerby, 1840). Holotype, figured by Sowerby (1832–41, *Murex* species 28, fig. 73). Height 57.5 mm, diameters 33, 30 mm. Locality unknown. The Saul label reads 'Scabrosus' and Saul Cat. No. is 24, the entry later amended by 'var Laciniatus Reeve'.

Murex similis Sowerby, 1841. (Sowerby, 1840). Holotype, figured by Sowerby (1832–41, *Murex* species 20, fig. 70), and Reeve (1845–46, pl. 25, fig. 108). Height 49 mm, diameters 25, 22 mm. Locality unknown. Saul Cat. No. 16. Sowerby's name is pre-occupied by *Murex similis* Schroeter, 1805. Clench and Farfante (1945) have identified the specimen as *Murex caillieti* var. *kugleri*.

Murex steeriae Reeve, 1845. (Reeve, 1845–46). Holotype, figured by Reeve (1845–46, pl. 8, fig. 28). Height 66.5 mm, diameters 52, 39 mm. Locality unknown. The specimen has the Saul label 'Steeriae' and Saul Cat. No. 109. The species was originally described by Reeve (1845a).

Murex trialatus Sowerby, 1841. (Sowerby, 1840). Holotype, figured by Sowerby (1832–41, *Murex* species 58, fig. 33), Reeve (1845–46, pl. 16, fig. 63 as *M. phyllopterus* Lamarck) and Sowerby (1879, pl. 11, fig. 107). Height 81 mm, diameters 53, 37 mm. Locality unknown. The Saul label reads 'Trialatus Sow Phyllopterus Lam' and there is a similar entry as Saul Cat. No. 47.

Murex tumulosus Sowerby, 1841. Holotype, figured by Sowerby (1832–41), *Murex* species 71, fig. 71). Though originally from Mus. Stainforth, a specimen in the Saul collection matches this illustration. The specimen is also figured by Reeve (1845–46, pl. 23, fig. 94). Height 91 mm, diameters 39, 34.5 mm. Locality unknown. Saul Cat. No. 124.

Ranella plicata Reeve, 1844d. Holotype, figured by Reeve (1844d, pl. 7, fig. 33). Height 34 mm, diameters 18, 15 mm. Locality unknown. The species was originally described by Reeve (1844e).

Strombus haemastoma Sowerby, 1842. Syntype. A specimen in the collection of Miss Saul is mentioned in the original description. The specimen is that figured by Reeve (1850–51, pl. 5, fig. 5). Height 13 mm, diameters 8, 5 mm. Locality unknown.

Triton ficioides Reeve, 1844b. Holotype, figured by Reeve (1844b, pl. 13, fig. 51). Height 55 mm, diameters 28, 21 mm. Locality Africa. The species was originally described by Reeve (1844c).

Triton sauliae Reeve, 1844b. Syntype. A syntype in the Saul collection is the specimen figured by Reeve (1844b, pl. 5, fig. 17a, b.). Height 106 mm, diameters 57, 48 mm. The species was originally described by Reeve (1844c).

Turbo articulatus Reeve, 1848. Syntype. Three syntypes were figured by Reeve (1848, pl. 9, fig. 3c, 39, 41). The Saul specimen (fig. 41) is of height 41 mm, diameters 34, 29 mm. Locality unknown. The other two specimens were from the Taylor collection.

Voluta beckii Broderip, 1836. Lectotype. Three syntypes were mentioned by Broderip (1836). The Saul specimen was designated the lectotype by Clench and Turner (1964).

Height 220 mm, diameters 90, 70 mm. Locality unknown. The specimen, which does not appear to have been previously figured, is illustrated in Plate 4.

BIVALVIA

Cardium australiensis Reeve, 1844. (Reeve, 1844–45). Holotype, a shell obtained by Harvey from Port Lincoln, South Australia, and figured by Reeve (1844–45, pl. 5, fig. 24). There is a specimen in the Saul collection which agrees in dimensions with this figure, but differs somewhat in markings. Length 27.5 mm, height 18 mm, width 11 mm. This shell is probably the holotype, but has no original label.

Cardium bechei Reeve, 1847. Syntype. This species was based on two single valves obtained at different localities. One is figured by Adams and Reeve (1848, pl. 32, fig. 12). The localities were given as 'Sooloo Seas. between the islands of Borneo and Mindanao' and 'from the Yellow Sea, thirty degrees north, at one of the islands of the Corean Archipelago'. The specimen in the Saul collection is a left valve inscribed within in pencil in Miss Saul's hand 'Belcher/21.3.48' and in another hand 'Sooloo Seas between Mindanao and Borneo'. This seems likely to be a syntype. Length 49 mm, height 52 mm. The figured specimen was a right valve of smaller size.

Cardium ferruginosum Reeve, 1845. (Reeve, 1844–45). Holotype, figured by Reeve (1844–45, pl. 20, fig. 106). Length 13 mm, height 13 mm, width 9 mm. Locality unknown.

Cardium oviputamen Reeve, 1844. (Reeve, 1844–45). Holotype, figured by Reeve (1844–45, pl. 7, fig. 36). Length 35.5 mm, height 40 mm, width 27 mm. Locality unknown. The species was originally described by Reeve (1844a).

Cardium pulicarium Reeve, 1845. (Reeve, 1844–45). Holotype, figured by Reeve (1844–45, pl. 19, fig. 102). Length 20 mm, height 21 mm, width 12.5 mm. Locality unknown.

Cardium rastrum Reeve, 1845. (Reeve, 1844–45). The holotype was figured by Reeve (1844–45, pl. 14, fig. 82). Not traced.

Cardium virgo Reeve, 1845. (Reeve, 1844–45). Holotype, figured by Reeve (1844–45, pl. 21, fig. 120). Length 16 mm, height 17 mm, width 13 mm. Locality unknown.

Crassatella castanea Reeve, 1842. Syntype. The specimen in the Saul collection is one of the syntypes mentioned by Reeve (1842). Length 92 mm, height 74 mm, width 35 mm.

Crassatella ornata Reeve, 1842. Holotype, figured by Reeve (1843, pl. 3, fig. 17). Length 26 mm, height 22.5 mm, width 14 mm. Locality unknown.

Crassatella triquetra Reeve, 1842. Syntype. The specimen figured by Reeve (1843, pl. 3, fig. 14) is a syntype contained in the Saul collection. Length 21 mm, height 18.5 mm, width 12 mm. Locality unknown.

Pecten filiosus Reeve, 1852. (Reeve, 1852–53). Holotype, figured by Reeve (1852–53, pl. 11, fig. 42). Length 62 mm, height 55 mm, width 22 mm. Moreton Bay, Australia.

Pecten histrionicus Gmelin, 1791. Neotype. The specimen figured by Reeve (1852–53, pl. 24, fig. 130) was designated neotype by Waller (1972). Length 24 mm, height 24 mm, width 6 mm. Locality cited by Reeve as 'Eastern Seas'.

Pecten modestus Reeve, 1852. (Reeve, 1852–53). Holotype. The Saul specimen described under this name as a new species by Reeve (1852–53, pl. 11, fig. 41) is of length 85 mm, height 70.5 mm, width 21 mm. Moreton Bay, Australia. Gmelin (1788–1793, p. 3331) validly published the name *Ostrea modesta* and referred to the figure in the vernacular work of Regenfuss (1758, pl. 5, fig. 55). Also Bosc (1802, p. 277) referred to the work of Regenfuss but not to Gmelin in his discussion of *Pecten modestus*. Reeve's name is therefore pre-occupied.

PLATE 4 (Opposite). Left: *Cypraea venusta* Sowerby 1847. Holotype, natural size. Right: *Voluta becki* Broderip 1836. Lectotype, $\times 3/4$ approx.

CYPRAEA VENUSTA AND VOLUTA BECKI



Pecten sericeus Hinds, 1844. (Hinds, 1844–45). Holotype, figured by Hinds (1844–45, pl. 17, fig. 1, 1a) and was obtained in the Bay of Panama. A specimen in the Saul collection is inscribed within in pencil in Miss Saul's hand 'Belcher 21.3–48' and agrees with Hinds' figure. Length 77 mm, height 73 mm, width 15 mm. The specimen is also figured by Reeve (1852–53, pl. 5, fig. 23).

Pecten spectabilis Reeve, 1853. (Reeve, 1852–53). Holotype, figured by Reeve (1852–53, pl. 29, fig. 128). Length 35 mm, height 23 mm, width 12 mm. Locality unknown. The specimen was discussed by Waller (1972).

ACKNOWLEDGEMENTS

Since the arrival of the Saul collection in Cambridge, various groups have received the attention of a number of workers. We are grateful for all their efforts. Those we know of are A. M. Bidder, H. C. Brock, R. C. Carter, A. H. Cooke, H. C. Fulton, S. F. Harmer, E. A. Kay, D. F. W. McMichael, T. Pain and C. R. C. Paul.

INDEX OF SPECIES NAMES

- | | |
|--|---|
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| <i>ambiguus</i> , <i>Murex</i> Reeve, 1845 | <i>oviputamen</i> , <i>Cardium</i> Reeve, 1844 |
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| <i>modesta</i> , <i>Ostrea</i> Gmelin, 1791 | <i>trizonata</i> , <i>Cypraea</i> Sowerby, 1870 |
| <i>modestus</i> , <i>Pecten</i> Reeve, 1852 | <i>tumulosus</i> , <i>Murex</i> Sowerby, 1841 |
| <i>nigrispinosus</i> , <i>Murex</i> Reeve, 1845 | <i>venusta</i> , <i>Cypraea</i> Sowerby, 1847 |
| <i>ornata</i> , <i>Crassatella</i> Reeve, 1842 | <i>virgo</i> , <i>Cardium</i> Reeve, 1845 |

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MOLLUSCA FROM AN INTERGLACIAL TUFA
IN EAST ANGLIA, WITH THE DESCRIPTION
OF A NEW SPECIES OF *LYRODISCUS*
PILSBRY (GASTROPODA: ZONITIDAE)

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(Read before the Society, 18 October 1975)

Abstract: The non-marine Mollusca of an interglacial tufa near Icklingham, W. Suffolk are listed. The fauna includes the extinct *Acicula diluviana* (Hocker) and a new species of *Lyrodiscus*, *L. skertchlyi*. *Lyrodiscus* Pilsbry 1893 (a subgenus of *Retinella*) is otherwise only known from the Canary Islands.

This paper describes a remarkable interglacial molluscan fauna from East Anglia. The stratigraphical context unfortunately remains somewhat unclear; nevertheless, the fauna is so unusual that interim publication seems warranted until such time as a fuller investigation of the site can be made.

The locality is an old brickyard, formerly known as Beeches Pit, about 1½ miles (2.5 km) ESE of Icklingham church, West Suffolk (NGR TL 798719). The pit was abandoned before 1890 and is now heavily overgrown. Sections recorded by the geologist S. B. J. Skertchly about 1877 showed up to about 12 feet (3.7 m) of 'loams, with carbonaceous seams . . . with shells of *Cyclas* [*Sphaerium*], *Pisidium*, *Bulimus* [*Bithynia*], *Helix* and *Succinea*' overlying chalky boulder clay (Whitaker *et al.* 1891, p. 79, fig. 18). Skertchly claimed that further boulder clay lay above the loams, although this point was disputed by others. Flint implements and mammalian bones also occurred.

In 1967, in a search for palaeolithic implements in stratified contexts in West Suffolk, Mr. G. de G. Sieveking (British Museum, Bloomsbury) cut some trenches in Beeches Pit. I examined these in company with Dr. C. Turner, and in July 1970 we measured the following section at about the middle of the north face of the pit:

0-55 cm	Modern soil, on gravel with large flints (?disturbed).
55-70 cm	Orange-brown silty loam (probably decalcified top of tufa).
70-95 cm	Yellow (Munsell 10YR 7/6) shelly calcareous tufa, with much orange iron-staining. Siltier and less tufaceous towards base. Some belemnite fragments at about 90 cm.
95-120 cm	Pale-grey (orange-mottled) plastic calcareous silt with scattered flints and chalk fragments. Shells (including <i>Pomatias elegans</i>) in top 5 cm.
120-145+ cm	Orange-brown chalky silt with abundant chalk fragments (?boulder clay).

All stratigraphical junctions were somewhat indistinct. A sample of about 3 kg from about 80 cm yielded the Mollusca listed below. Although surface preservation is excellent the shells are extremely crushed, making determination difficult. The numbers refer to apical fragments unless stated otherwise.

<i>Valvata cristata</i> Müller	175	<i>Retinella</i> (<i>Lyrodiscus</i>) <i>skertchlyi</i> sp. nov.	37
<i>Pomatias elegans</i> (Müller)	25	<i>Oxychilus</i> cf. <i>cellarius</i> (Müller)	3
<i>Acicula diluviana</i> (Hocker)	5	<i>Oxychilus</i> sp. (not <i>cellarius</i>)	2
<i>Acicula polita</i> (Hartmann)	64	<i>Zonitoides excavatus</i> (Alder)	20
<i>Bithynia</i> sp.	1 op	<i>Milax</i> sp.	7
<i>Carychium minimum</i> Müller	7	<i>Deroceras</i> / <i>Limax</i>	12
<i>Carychium tridentatum</i> (Risso)	78	<i>Euconulus fulvus</i> (Müller)	10
<i>Planorbis planorbis</i> (Linné)	2	<i>Cochlodina laminata</i> (Montagu)	1 m
<i>Bathyomphalus contortus</i> (Linné)	1	<i>Cochlodina</i> sp.	5
<i>Hippeutis complanatus</i> (Linné)	2	<i>Ruthenica filograna</i> (Rossmässler)	f
<i>Azeca goodalli</i> (Férussac)	92 m	<i>Clausilia parvula</i> Férussac	1 m
<i>Cochlicopa</i> sp.	2 m	<i>Clausilia bidentata</i> (Ström)	2 m
<i>Vertigo pusilla</i> Müller	6	<i>Clausilia</i> cf. <i>pumila</i> Pfeiffer	fs
cf. <i>Leiostyla anglica</i> (Wood)	3	<i>Balea perversa</i> (Linné)	1
<i>Vallonia costata</i> (Müller)	4	Clausiliidae indet.	28
<i>Acanthinula aculeata</i> (Müller)	50	cf. <i>Zenobiella subrufescens</i> (Miller)	fs
<i>Ena montana</i> (Draparnaud)	2 m	<i>Helicodonta obvoluta</i> (Müller)	11
<i>Punctum pygmaeum</i> (Draparnaud)	30	<i>Helicigona lapicida</i> (Linné)	2
<i>Discus rotundatus</i> (Müller)	289	<i>Arianta arbustorum</i> (Linné)	fs
<i>Vitrea</i> cf. <i>crystallina</i> (Müller)	101	<i>Arianta</i> / <i>Cepaea</i>	3
<i>Vitrea contracta</i> (Westerlund)	17	<i>Cepaea nemoralis</i> (Linné)	fs
<i>Nesovitrea hammonis</i> (Ström)	3	<i>Sphaerium corneum</i> (Linné)	fs
<i>Aegopinella pura</i> (Alder)	98	<i>Pisidium obtusale</i> (Lamarck)	7
<i>Aegopinella</i> cf. <i>nitidula</i> (Draparnaud)	78		

(m = mouth fragment; f(s) = other fragment(s); op = operculum).

The assemblage shows that the tufa formed in a temperate forest, in association with pools probably fed by springs. The presence of *Bithynia* and *Sphaerium corneum* suggests that perhaps deeper water lay nearby. The terrestrial fauna is of highly remarkable character and strongly resembles that of a tufa near Hitchin, Hertfordshire, probably of Hoxnian interglacial age (Kerney, 1959). The central European clausiliid *Ruthenica filograna* and the extinct *Acicula diluviana* (Kerney, 1959; figs. 2, 3, 6) are known in Britain only from that deposit. The central European forest species *Acicula polita* is known additionally in Britain only from the late Hoxnian Middle Gravels of Barnfield Pit, Swanscombe, Kent (Kerney, 1971). Abroad, the nearest parallel is provided by the fauna of interglacial tufas at Schmiechen, near Ulm in S.W. Germany (Dehm, 1951), also considered to be of Hoxnian ('Mindel-Riss') age.

An ascription of the Icklingham tufa to the Hoxnian interglacial period must however for the present remain somewhat inferential. No pollen could be found, though carefully searched for by Dr. Turner. Stratigraphically, all that is clear is that the deposit (and that of Hitchin) post-dates the earliest (?only) boulder clay of southern East Anglia, formed during the Anglian (Lowestoft) glacial stage, immediately preceding the Hoxnian interglacial (Turner in Mitchell *et al.* 1973: 9).

The most remarkable and surprising feature of the Icklingham fauna remains to be mentioned: the common presence of a hitherto unknown zonitid belonging to the section *Lyrodiscus* Pilsbry, previously believed to be endemic to the Canary Islands. *Lyrodiscus*, regarded by Zilch (*in* Wenz and Zilch, 1959-60, 251) and by Forcart (1960) as a subgenus of *Retinella*, was originally defined by Pilsbry (*in* Tryon and Pilsbry, 1893, 9: 48) as follows:

'Shell depressed, with large open umbilicus and low-convex spire, in form being like *Patula* [*Discus*]; surface sculptured with slight growth-lines and numerous elevated cuticular spiral threads. Type *H. circumsesta* Shuttlew.'

A lectotype of *Helix circumsesta* from Tenerife is figured by Forcart (1960, pl. 2, fig. 7).

Only fragmentary and juvenile material could be extracted at Icklingham, but this leaves no doubt that an ascription to *Lyrodiscus* is correct. The sculpture is highly dis-

tinctive and recognizable even in small fragments: the rather coarse growth ridges are crossed by a system of well-spaced parallel *raised* spiral lines, looking rather like fine scars left by half-healed scratches (Fig. 3). They are quite different from the delicate spiral striations seen in many Zonitidae (e.g., in *Aegopinella pura*). Wollaston (1878, pp. 317–20) gives three species from the Canaries: *Retinella* (*Lyrodiscus*) *circumsessa* (Shuttleworth), *R.* (*L.*) *osoriensis* (Wollaston) and *R.* (*L.*) *lenis* (Shuttleworth). I have examined specimens of all three in the British Museum collections, but the fossil form does not correspond precisely with any of them and I therefore describe it here as a new species.

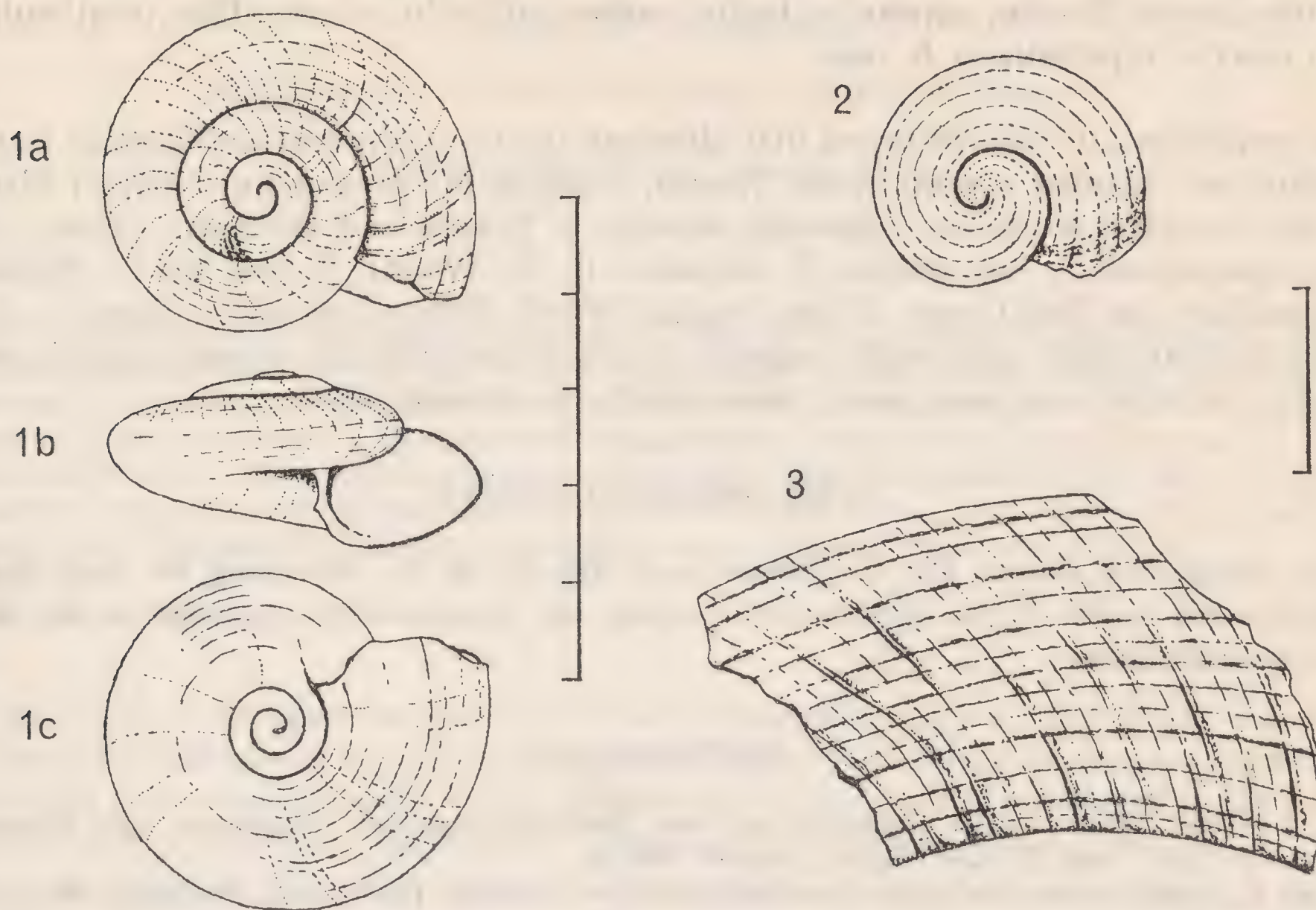


Fig. 1 to 3. *Retinella* (*Lyrodiscus*) *skertchlyi* sp. nov. 1, holotype (BMNH PD GG 9140); 2, embryonal shell; 3, upper surface of fragment of later whorl. Scales in millimetres.

Retinella (*Lyrodiscus*) *skertchlyi* sp. nov.

Description. Discoidal, bluntly keeled when young, becoming more rounded at the periphery when adult. Suture well-defined, but not deep. Umbilicus very large, accounting for at least one-fifth the width of the base. Adult size estimated (from fragments) at about 4 to $4\frac{1}{4}$ whorls, and attaining about 8.0 mm in diameter (holotype (Fig. 1) 4.1 mm; largest specimen recovered 5.6 mm). Last whorl apparently slightly expanded (as in *Aegopinella*), though it is difficult to be certain on this point. Lip sharp and simple, not reflected. Shell rather thin, glossy, apparently quite colourless. Growth-lines rather coarse and irregular, crossed by numerous fine raised spiral lines, about equally developed on both upper and lower surfaces. The otherwise smooth embryonal shell (Fig. 2) also shows these lines. The junction between the embryonal shell and the later whorls is sometimes marked by a slight irregularity in growth (Figs. 1a and 2).

The species is named after S. B. J. Skertchly (1851–1926), a pioneer in the study of the Pleistocene geology of East Anglia.

Occurrence. Interglacial tufa, Icklingham, Suffolk: 37 juveniles or apical fragments, and

78 other fragments. Holotype (Fig. 1) British Museum (Natural History) PD GG 9140; paratype (fragmentary shell 5.6 mm in diameter) PD GG 9141.

Related species. *R. circumssa* (Tenerife, La Palma) is clearly distinct. The whorls are narrower and more tightly coiled, and are more strongly convex, with a correspondingly deeper suture. The last whorl is not expanded or scarcely so. The sculpture is like that of *R. skertchlyi*. The two closely similar species *R. lenis* (La Palma, Hierro) and *R. osoriensis* (Gran Canaria) resemble *R. skertchlyi* more nearly in general form, although in both the rate of expansion of the whorls is slightly less (i.e., the coiling is tighter) and the suture is a little deeper. Keeling appears to be lost rather earlier in growth. The spiral sculpture is also weaker, especially in *R. lenis*.

In conclusion, it must be noted that although the occurrence of *Lyrodiscus* in England is unexpected, another zonitid genus, *Janulus*, living at the present time only in Madeira and the Canaries, occurs in Oligocene deposits in France and Germany (Wenz, 1923) and is represented by two species (*J. suttonensis* (S. V. Wood), *J. rysus* (S. V. Wood)) in the Coralline and Red Craggs of East Anglia (Wood, 1848, 1: 4; 1872, suppt. 1: 2). So it may be that other apparently endemic snails of the Atlantic oceanic islands are in fact relics of what were once much more widely distributed taxa.

ACKNOWLEDGEMENTS

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THE MARINE MOLLUSCA OF LIVERPOOL BAY (IRISH SEA)

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(Read before the Society, 15 November 1975)

Abstract: Comparison of the distributions of shell assemblages and living molluscan populations in Liverpool Bay, indicates considerable offshore and onshore transportation of shells and preferential accumulation in the intertidal zone. The different depths from which moribund and empty shells are derived suggest two separate modes of transportation. Instantaneous transportation occurs in short, infrequent periods of high energy conditions at the sediment/water interface and produces high density, low diversity shell assemblages. Progressive transportation occurs more frequently and produces low density, high diversity shell assemblages. A systematic list of the marine Mollusca of collecting areas in Liverpool Bay is also presented.

This work was undertaken as part of doctoral research to identify and relate the distribution and abundance of the empty shell assemblages to the living molluscan populations from which they were derived. The area discussed in this paper is situated in the south-eastern corner of Liverpool Bay and is within a 30 kilometre radius of the mouth of the Dee estuary (Fig. 1). The Bay has a shallow, gently sloping floor of sandy and muddy gravel bordered to the south and east by inshore areas of mobile, clean sand. Four specific areas of the Bay have been selected; central Liverpool Bay (10-40 metres deep), north Wirral offshore (Low Water Spring tides (L.W.S.)—15 metres), south-west Lancashire offshore (L.W.S.—10 metres) and intertidal (L.W.S.—High Water Spring tides (H.W.S.)) and these are regarded as possessing molluscan populations and shell assemblages typical of the depth zones which they occupy.

The accompanying occurrence list is compiled from several surveys during the last fifteen years, the results of which are not generally available (Sly, 1966; Rees *et al* , 1972 and unpublished; Eagle, 1973, 1974 and unpublished; Lingwood, 1976 and unpublished). Shell status is in accordance with the recording scheme for marine molluscs, i.e. *A*—molluscs living *in situ*, *B*—shell fresh or with animal remains, *C*—worn shell or single valves. The depth ranges of the individual species are those of the denser living populations derived, where possible, from occurrences in Liverpool Bay and the literature (Forbes and Hanley, 1853; Jeffreys, 1863-1869; Marine Biological Association, 1957; Allen, 1962; Bruce *et al.*, 1963; Tebble, 1966; Clay, 1967). These ranges have been simplified into four depth zones, i.e. intertidal (H.W.S.—L.W.S.), subtidal (L.W.S.—10 m.), offshore (10-25 m.), and deeper (25 m. +) based on the most frequently observed ranges. The depths from which the shell assemblages have been derived are expressed as the average number of species living in the four zones. Thus, widespread species are equally distributed between the zones they are known, or assumed to inhabit, so that they are not preferentially weighted against more restricted species.

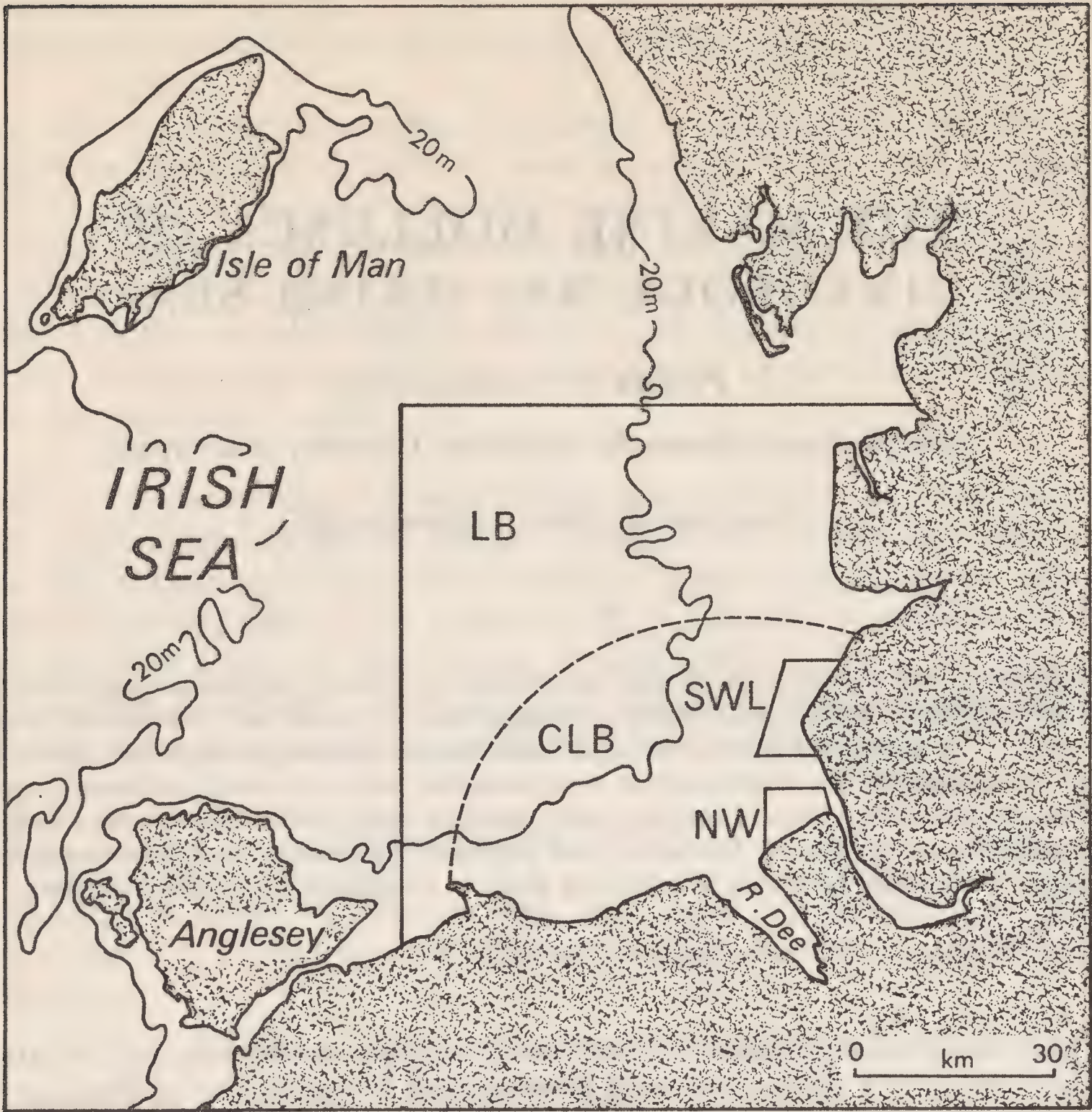


Fig. 1. Location Map of Liverpool Bay. LB Liverpool Bay (Census area 14); --- CLB Central Liverpool Bay; NW North Wirral Offshore Area; SWL South West Lancashire Offshore and Intertidal.

TABLE 1
Geographical distribution of number of species according to status

STATUS	GASTROPODA				BIVALVIA				TOTAL			
	Lancs.				Lancs.				Lancs.			
	I	S	Wir.	CLB.	I	S	Wir.	CLB.	I	S	Wir.	CLB.
A	2	2	3	8	8	15	19	54	10	17	22	62
B	1	0	0	0	18	2	6	3	19	2	6	3
C	20	3	5	14	35	18	25	35	55	21	30	49
A/C												
Ratio	1:10	1:1.5	1:1.7	1:1.7	1:4.4	1:1.2	1:1.3	1:0.7	1:5.5	1:1.2	1:1.4	1:0.8

Lancs.—S.W. Lancashire coast, Intertidal (I) and Subtidal (S); Wir.—North Wirral Subtidal; CLB—Central Liverpool Bay.

DISTRIBUTION

The number of living gastropod and bivalve species (status *A*) increases with depth (Table 1). This is partly a function of the increasing size of the sample area but also the lower energy conditions and greater variety of benthonic habitats. Status *B* shells are mostly recorded from the foreshore during storms as they are not easy to collect offshore in such conditions. The large number of empty shells in deeper water is attributed to

LINGWOOD: MARINE MOLLUSCA OF LIVERPOOL BAY

the greater faunal diversity offshore (Rees *et al.*, 1972). The large number of species in the intertidal zone is due to the influx of species not indigenous to the foreshore, as shown by the low *A/C* ratio, suggesting preferential accumulation in the intertidal zone. The consistently lower *A/C* ratio of gastropods compared to that of bivalves suggests that the former are in general more robust and therefore able to withstand the rigours of transportation.

TABLE 2
Mean numbers and percentages of species from each depth zone of status *C* shells from various parts of Liverpool Bay

	DEPTH ZONES	S.W. LANCS.				WIR.	CLB.	ALL AREAS	
		I		S					
intertidal		*5.0	(9)	4.0	(20)	4.0	(14)	4.0	(9)
subtidal	(0-10 m.)	13.3	(25)	*7.5	(38)	*7.3	(38)	8.8	(20)
offshore	(10-25 m.)	16.2	(31)	5.0	(25)	*8.8	(32)	12.1	(28)
deep	(25 + m.)	18.3	(35)	3.5	(17)	7.3	(26)	18.6	(43)
								25.5	(39)

Abbreviations as in Table 1; () percentage of species derived from each depth zone; maximum mean number and maximum percentage per sample in bold; * species indigenous to sample area.

TRANSPORTATION

Comparison of the distribution of the number of species among the four depth zones shows that all areas contain exotic species, i.e. those that do not normally inhabit the areas (Table 2). The proportion of exotic species is greatest intertidally (91%) and decreases offshore to 28% in deep water. Offshore the species indigenous to an area form the largest group from any one depth zone. Thus subtidal species in the south-west Lancashire subtidal area are numerically (7.5) and proportionally (38%) more important than species derived from any other depth zone. Subtidal and offshore species are most important in the north Wirral area, and offshore and deep species most important in the centre of the Bay. However, the majority of the species in the intertidal assemblage are derived predominantly from the offshore and deep zones. The proportion of species from each depth zone is similar to those from all the areas combined. This suggests that shells of any one depth zone are not preferentially deposited on the south-west Lancashire foreshore.

TABLE 3
Mean number of species in the S.W. Lancashire foreshore from each depth zone of status *B* shells on the S.W. Lancashire foreshore

	DEPTH ZONES	B	B/C
intertidal		2.0	1:2.5
subtidal	(0-10 m.)	6.3	1:2.0
offshore	(10-25 m.)	5.8	1:2.5
deep	(25 + m.)	3.8	1:4.2
		18.0	

Abbreviations as in Table 1.

Moribund and dead individuals (status *B*) cast up during storms appear to be derived from closer inshore (Table 3). The ratio of status *B* to status *C* species on the south-west Lancashire foreshore suggests that the former are preferentially derived from the subtidal zone. The flesh of dead molluscs degrades in a matter of days, therefore status *B* shells

must have been eroded and transported on to the beach during the period of the storm. The low ratio of shells from depths greater than subtidal indicates that the flesh from these has already disintegrated because of the greater time interval between death and arrival on the foreshore. The low B/C ratio in the intertidal zone is possibly due to the greater adaptation of intertidal species to high energy conditions.

It is suggested therefore that two modes of wave-induced transportation can be distinguished; instantaneous and progressive. Instantaneous transport occurs in infrequent periods of high energy at the sediment/water interface, e.g. during storms, and transports a large number of shells from a restricted range of inshore species resulting in an assemblage with a high B/C ratio. Progressive transportation occurs more frequently in lower energy conditions and transports fewer shells of a wide range of species, providing the shells are sufficiently robust to survive, resulting in an assemblage with a low B/C ratio. Offshore progressive transportation will only occur intermittently during storms.

The frequency with which shells will be moved increases with the proximity to the coast (i.e. with decreasing depths). Thus offshore shells, because of the protection afforded by the depth of water, will be subject only to progressive transportation. Closer inshore progressive transportation will be more frequent with the addition of infrequent instantaneous transportation during periods of very high energy on the sea surface. In very shallow water shells may be liable to almost continuous progressive transportation and frequent instantaneous transportation even in comparatively calm conditions.

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SYSTEMATIC LIST OF THE MOLLUSCA OF LIVERPOOL BAY

		DEPTH	SW LANGS			
		GROUP	I.	S.	Wir.	C.L.B.
GASTROPODA						
G20	<i>Calliostoma zizyphinum</i> (Lamarck)	I	—	—	—	C
G24	<i>Gibbula tumida</i> (Montagu)	SO	—	—	—	C
G25	<i>Gibbula cineraria</i> (L.)		—	—	—	C
G36	<i>Tricolia pullus</i> (da Costa)	SO	—	—	—	C
G42	<i>Littorina littorea</i> (L.)	I	C	C	C	C
G48	<i>Hydrobia ulvae</i> Pennant	I	AC	C	—	—
G87	<i>Turritella communis</i> Risso	D	C	—	C	C
G100	<i>Clathrus clathrus</i> (L.)		C	—	—	—
G101	<i>Clathrus turtonis</i> (Turton)	OD	C	—	—	C
G111	<i>Eulima glabra</i> (da Costa)		C	—	—	—
G170	<i>Aporrhais pespelecani</i> (L.)	D	C	—	—	C
G176	<i>Natica catena</i> (da Costa)	OD	C	—	—	C
G177	<i>Natica alderi</i> Forbes	SO	AC	AC	AC	AC
G184	<i>Trivia arctica</i> (Pulteney)	D	C	—	—	C
G187	<i>Trophon truncatus</i> (Ström)	OD	—	—	—	C
G192	<i>Ocenebra erinacea</i> (L.)	D	C	—	—	—
G199	<i>Colus gracilis</i> (da Costa)	OD	—	—	—	A
G203	<i>Neptunea antiqua</i> (L.)	OD	C	—	—	A
G204	<i>Buccinum undatum</i> L.	OD	BC	—	AC	AC
G208	<i>Nassarius incrassatus</i> (Ström)	OD	—	—	—	C
G224	<i>Philibertia gracilis</i> (Montagu)	OD	C	—	—	—
G228	<i>Philibertia linearis</i> (Montagu)	OD	C	—	—	—
G230	<i>Acteon tornatalis</i> (L.)	SOD	C	—	—	A
G239	<i>Retusa alba</i> (Kanmacher)	SOD	C	—	—	—

LINGWOOD: MARINE MOLLUSCA OF LIVERPOOL BAY

	DEPTH GROUP	SW LANCS		WIR.	C.L.B.
		I.	S.		
G243 <i>Cylichna cylindracea</i> (Pennant)	OD	C	—	—	A
G245 <i>Scaphander lignarius</i> (L.)	SOD	C	—	—	A
G247 <i>Philine quadripartita</i> (Ascanius)	OD	C	A	AC	A
SCAPHODA					
S1 <i>Dentalium entalis</i> L.	OD	—	—	—	C
BIVALVIA					
L1 <i>Nucula sulcata</i> Brown	OD	—	—	—	A
L2 <i>Nucula nucleus</i> (L.)	OD	—	—	—	A
L3 <i>Nucula hanleyi</i> Winckworth	OD	—	—	—	A
L4 <i>Nucula turgida</i> Leckenby & Marshall	ODod	C	AC	C	AC
L12 <i>Glycimeris glycimeris</i> da Costa	D	—	—	—	C
L16 <i>Anomia ephippium</i> L.	SOD	—	—	—	AC
L20 <i>Mytilus edulis</i> L.	S	ABC	ABC	C	AC
L22 <i>Modiolus modiolus</i> (L.)	OD	C	—	AC	A
L26 <i>Modiolus phaseolinus</i> (Philippi)		—	—	—	A
L35 <i>Ostrea edulis</i> L.	SOD	C	—	—	A
L42 <i>Chlamys varia</i> (L.)	D	C	C	C	AC
L43 <i>Chlamys distorta</i> (da Costa)	D	—	—	—	C
L44 <i>Chlamys opercularis</i> (L.)	D	C	—	A	AC
L47 <i>Chlamys tigerina</i> (Müller)		—	—	—	C
L52 <i>Lima loscombi</i> Sowerby	D	—	—	—	AC
L56 <i>Astarte sulcata</i> (da Costa)	OD	—	—	—	A
L60 <i>Thyasira flexuosa</i> (Montagu)	OD	—	—	—	A
L64 <i>Loripes lucinalis</i> (Lamarck)		C	—	—	—
L71 <i>Turtonia minuta</i> (Fabricius)	I	—	—	—	A
L72 <i>Lepton squamosum</i> (Montagu)		—	—	—	A
L73 <i>Lepton nitidum</i> Turton	D	—	—	—	A
L78 <i>Montacuta substriata</i> (Montagu)	OD	—	—	—	A
L79 <i>Montacuta ferruginosa</i> (Montagu)	OD	—	—	—	A
L80 <i>Mysella bidentata</i> (Montagu)	ODsod	B	A	A	A
L83 <i>Devonia perrieri</i> (Malard)	—	—	—	—	A
L84 <i>Cyprina islandica</i> (L.)	OD	C	—	—	A
L87 <i>Acanthocardia echinata</i> L.	OD	BC	—	AC	C
L91 <i>Parvicardium scabrum</i> Philippi	OD	—	—	—	C
L93 <i>Cerastoderma edule</i> L.	I	ABC	C	C	C
L94 <i>Laevicardium crassum</i> Gmelin	D	—	—	—	ABC
L95 <i>Dosinea exoleta</i> (L.)	SOD	—	A	AC	A
L96 <i>Dosinea lupinus</i> (Montagu)	SOD	A	—	—	A
L100 <i>Venus casina</i> L.	OD	—	—	—	C
L101 <i>Venus ovata</i> Pennant	OD	C	C	AC	AC
L102 <i>Venus fasciata</i> (da Costa)	OD	—	—	—	C
L103 <i>Venus striatula</i> (da Costa)	SOso	ABC	ABC	AC	AC
L105 <i>Venerupis rhomboides</i> (Pennant)	Dod	B	—	—	A
L106 <i>Venerupis pullastra</i> (Montagu)	OD	B	—	A	—
L111 <i>Mysia undata</i> (Pennant)	OD	C	—	—	A
L112 <i>Donax vittatus</i> (da Costa)	Ss	ABC	AC	ABC	AC
L116 <i>Tellina tenuis</i> (da Costa)	I	ABC	AC	ABC	C
L117 <i>Tellina fabula</i> Gmelin	SOs	ABC	AC	ABC	A
L118 <i>Tellina donacina</i> L.	ODd	—	—	—	A
L119 <i>Tellina pygmaea</i> Lovén	ODod	—	—	—	A
L120 <i>Arcopagia crassa</i> Pennant		—	—	—	A
L123 <i>Macoma balthica</i> (L.)	I	ABC	C	ABC	C
L124 <i>Scrobicularia plana</i> (da Costa)	I	C	—	C	—
L126 <i>Abra alba</i> (W. Wood)	SO	ABC	AC	ABC	AC
L127 <i>Abra nitida</i> (Müller)	OD	BC	—	C	ABC
L128 <i>Abra prismatica</i> (Montagu)	OD	—	—	AC	A
L129 <i>Gari fervensis</i> (Gmelin)	SOod	BC	—	AC	AC

L135	<i>Pharus legumen</i> (L.)	SODs	C	C	C	AC
L136	<i>Cultellus pellucidus</i> (Pennant)	D	C	—	A	AC
L137	<i>Ensis ensis</i> (L.)	SO	BC	A	—	A
L138	<i>Ensis arcuatus</i> (Jeffreys)	SO	C	—	—	A
L139	<i>Ensis siliqua</i> (L.)	SO	C	—	C	—
	<i>Ensis</i> sp. (fragments)	—	C	C	C	C
L141	<i>Mactra corallina</i> (L.)	SO	BC	AC	C	AC
L142	<i>Spisula elliptica</i> (Brown)	OD	BC	AC	ABC	AC
L143	<i>Spisula solida</i> (L.)	S	—	—	—	A
L144	<i>Spisula subtruncata</i> (da Costa)	SO	C	—	—	AC
L145	<i>Lutraria lutraria</i> (L.)	SO	C	C	—	C
	<i>Lutraria angustior</i> (Philippi)		—	—	—	BC
L147	<i>Mya truncata</i> L.	SOD	C	—	—	A
L148	<i>Mya arenaria</i> L.	SOD	C	A	A	AC
L150	<i>Corbula gibba</i> (Olivi)	ODod	C	AC	C	AC
L154	<i>Saxicavella jeffreysi</i> Winckworth	OD	—	—	—	A
L157	<i>Barnea candida</i> (L.)	S	BC	C	C	C
L159	<i>Zirfea crispata</i> (L.)	S	C	—	—	—
L169	<i>Cochlodesma praetenu</i> (Pulteney)		C	—	—	A
L170	<i>Thracia phaseolina</i> (Lamarck)	SOD	C	A	A	A
L171	<i>Thracia villosiuscula</i> (Macgillivray)	SO	—	—	—	A
L175	<i>Lyonsia norwegica</i> (Gmelin)	D	—	—	—	A
L176	<i>Pandora albida</i> (Röding)		—	—	—	A

Species names and numbers according to Winckworth (1932). Shell status: A, living; B, shell empty or with animal remains; C, worn shell or single valves. Depth of denser populations: lower case letters, Central Liverpool Bay; upper case letters, from literature (see text); I, Intertidal, HWS–LWS (High Water Springs to Low Water Springs); S, Subtidal, LWS–10 m.; O, Offshore, 10 m.–25 m.; D, Deep, 25 m. + m.

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THE MOLLUSCA OF SOME POOR FENS IN CO. CORK, IRELAND

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Abstract: The Mollusca of some acid fens in south-west Ireland are listed together with the vegetation at collection sites. The fens all produced more extensive mollusc faunas (8-18 species) than was expected, possibly due to the ameliorating effects of the Atlantic climate with its high precipitation and mild winters.

The fens of Ireland present some of the most interesting habitats in the country to the student of terrestrial Mollusca. In the past particular attention has been paid to the rarer species of *Vertigo* including *V. angustior* Jeffreys (Norris and Colville, 1974), *V. geyeri* Lindholm (Norris and Pickerell, 1972) and *V. lilljeborgi* (Westerlund) (Kevan and Waterston, 1933). General studies have been few, and absolute population estimates have yet to be made of Mollusca in an Irish fen. I suspect that the maximum density of individuals may prove to be even higher than in woodland sites, although the species diversity may be lower (compare Mason, 1974).

The extreme richness of the calcareous sites has naturally led to some neglect of the more acidic and species-poor areas. The present work is a contribution to the study of the effect of reduced base status on the occurrence of individual species.

The study sites are situated in W. Cork (Fig. 1) on an area of Devonian and Carboniferous strata giving rise to neutral or acidic soils. The climate is intensely 'atlantic' with the heaviest precipitation and the mildest winters in Ireland. The high rainfall leads to severe leaching and the development of highly acidic blanket bog. The oligotrophic bogs are barren of Mollusca except for the occasional *Arion ater*. Local enrichment allows the development of poor fen conditions, with an impoverished but interesting fauna. Each study site was a 10 by 10 m plot chosen on the basis of its vegetation. The vegetation and Mollusca present are listed in Tables 1 and 2, respectively.

Site 1 was situated near Coolkellure (Irish National Grid Reference W1954) at a height of 500 ft. (162 m) above sea level with a slight slope ($<5^\circ$) and southerly aspect. Readings of pH taken with the electrode of a portable meter inserted in the moss carpet were in the range 4.4-4.7. The vegetation was characterized by the presence of *Erica tetralix*, *Ulex gallii* and *Narthecium ossifragum* with a paucity of dicotyledon herbs. The mosses included the strongly calcifuge *Pleurozium schreberi* and *Sphagnum plumulosum*, which is one of the commonest species of blanket bogs. This vegetation sounds most unpromising for Mollusca, but in fact 8 species were obtained. In eastern Britain such an acid site would yield few molluscs, but here the favourable climatic conditions exert fewer constraints upon species distribution. The vegetation structure is such that there are two main strata, an upper layer of angiosperms and a lower layer of mosses and decaying plant material. *Cepaea nemoralis*, *Zenobiella subrufescens* and *Columella aspera* were swept from the angiosperm vegetation, whereas the other species were obtained by sieving the

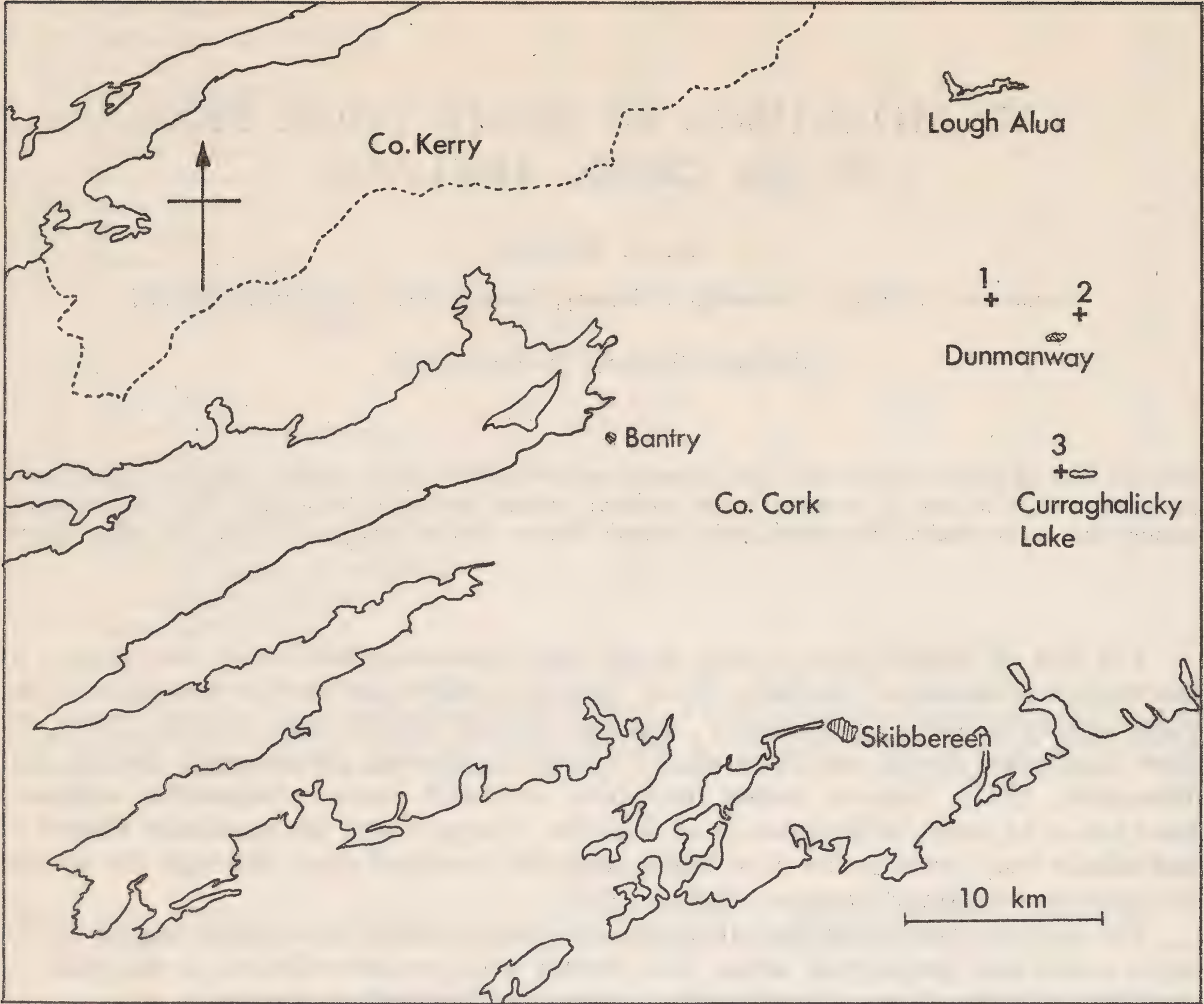


Fig. 1. Map of S.W. Cork to show the location of the three poor fen sites.

TABLE 1. Vegetation of the poor fens in Co. Cork, species presence indicated by +. The nomenclature of vascular plants follows Clapham, Tutin and Warburg (1964), that of bryophytes Watson (1968).

VASCULAR PLANTS

	1	2	3A	3B
<i>Erica tetralix</i> L.	+	.	.	.
<i>Hedera helix</i> L.	.	.	.	+
<i>Myrica gale</i> L.	+	.	+	+
<i>Salix aurita</i> L.	.	+	.	+
<i>Ulex gallii</i> Planch.	+	.	.	.
<i>Dryopteris carthusiana</i> (Villar) H. P. Fuchs	.	.	.	+
<i>Equisetum fluviatile</i> L.	.	+	.	+
<i>Osmunda regalis</i> L.	.	+	+	.
<i>Deschampsia caespitosa</i> (L.) Beauv.	.	.	+	.
<i>Molinia caerulea</i> (L.) Moench	+	+	+	.
<i>Juncus acutiflorus</i> Ehrh. ex Hoffm.	+	+	+	+
<i>Menyanthes trifolia</i> L.	.	+	+	.
<i>Narthecium ossifragum</i> (L.) Huds.	+	.	.	.
<i>Angelica sylvestris</i> L.	.	+	+	+
<i>Filipendula ulmaria</i> (L.) Maxim.	.	+	+	+
<i>Galium palustre</i> L.	.	.	.	+
<i>Hydrocotyle vulgaris</i> L.	.	+	.	.

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<i>Lotus pedunculatus</i> Cav.	.	+	+	.
<i>Lycopus europaeus</i> L.	.	.	.	+
<i>Potentilla erecta</i> (L.) Rausch.	+	.	+	.
<i>P. palustris</i> (L.) Scop.	.	+	+	.
<i>Succisa pratensis</i> Moench	+	+	+	.
<i>Viola palustris</i> L.	.	.	+	.
MOSSES				
<i>Acrocladium cuspidatum</i> (Hedw.) Lindb.	.	+	+	+
<i>Brachythecium rutabulum</i> (Hedw.) B., S. & G.	.	+	.	+
<i>Eurynchium praelongum</i> (Hedw.) Hobk.	.	.	+	+
<i>Hylocomium splendens</i> (Hedw.) B., S. & G.	+	.	.	.
<i>Pleurozium schreberi</i> (Brid.) Mitt.	+	.	.	.
<i>Polytrichum commune</i> Hedw.	.	.	+	.
<i>Pseudoscleropodium purum</i> (Hedw.) Fleisch.	.	+	.	.
<i>Rhytidiadelphus loreus</i> (Hedw.) Warnst.	+	.	.	.
<i>R. squarrosus</i> (Hedw.) Warnst.	.	+	.	.
<i>Sphagnum plumulosum</i> Röll.	+	.	.	.
<i>S. palustre</i> L.	+	.	.	.
<i>S. recurvum</i> P. Beauv.	+	+	+	.
<i>S. subsecundum</i> Nees var. <i>inundatum</i>	.	.	+	.
<i>Ulotia crispa</i> (Hedw.) Brid.	.	.	.	+
<i>U. phyllantha</i> Brid.	.	.	.	+

TABLE 2. Mollusca from the poor fens in Co. Cork, species presence indicated by +.

	1	2	3A	3B
<i>Carychium minimum</i> Müller seg.	.	+	+	.
<i>Aegopinella nitidula</i> (Draparnaud)	.	+	.	.
<i>Arion ater</i> (Linnaeus) ssp. <i>ater</i>	+	.	+	.
<i>A. intermedius</i> Normand	.	+	+	.
<i>A. subfuscus</i> (Draparnaud)	.	+	+	.
<i>Cepaea nemoralis</i> (Linnaeus)	+	+	+	.
<i>Cochlicopa lubrica</i> (Müller) seg.	.	+	+	+
<i>Columella aspera</i> Waldén	+	+	+	.
<i>Deroceras laeve</i> (Müller)	+	+	+	.
<i>D. reticulatum</i> (Müller)	.	+	+	.
<i>Euconulus fulvus</i> (Müller)	+	+	+	+
<i>Leiostyla anglica</i> (Wood)	.	+	.	.
<i>Nesovitrea hammonis</i> (Ström)	+	+	+	+
<i>Punctum pygmaeum</i> (Draparnaud)	.	.	+	+
<i>Oxyloma pfeifferi</i> (Rossmässler)	.	+	+	+
<i>Vertigo antivertigo</i> (Draparnaud)	+	+	.	.
<i>V. pygmaea</i> (Draparnaud)	.	+	.	.
<i>V. substriata</i> (Jeffreys)	.	+	+	+
<i>Vitrea crystallina</i> (Müller) seg.	.	.	.	+
<i>Zenobiella subrufescens</i> (Miller)	+	.	.	.
<i>Zonitoides nitidus</i> (Müller)	.	+	.	.
<i>Pisidium personatum</i> Malm	.	+	.	+

moss carpet. The helicids live in the upper layer, seldom needing to take shelter from dehydration because of the constantly humid micro-climate. They need have little contact with the highly acid ground layer. The occurrence of *Vertigo antivertigo* at such low pH is of note.

Site 2 was 2 km N. of Dunmanway (W2354) at a height of 250 ft (76 m), level and with a pH range of 4.8–5.1. *Osmunda regalis* was present, whilst *Angelica sylvestris*, *Filipendula ulmaria* and *Acrocladium cuspidatum* indicated a more base-rich situation. *S. recurvum*, the only species of *Sphagnum* at this site, is the species most tolerant to mineral enrichment. The mollusc fauna was richer and *Aegopinella nitidula*, *Leiostyla anglica*, *Vertigo pygmaea* and *Zonitoides nitidus* occurred only at this site.

Site 3 was at the west end of Curraghally Lake (W2346) at a height of 350 ft (108 m) and was level. Plot 3A had a pH range of 4.5–4.8 and was dominated by tussocks of *Deschampsia caespitosa* and *Molinia caerulea*. There were again some indications of base enrichment, *Sphagnum subsecundum* being a typical poor fen species; but the presence of *Polytrichum commune* indicated at least local intense acidity. The fauna was unremarkable, except perhaps for the presence of *Carychium minimum* below pH 5.0. The assemblage could be taken as characteristic of poor fens all over the western part of British Isles. Plot 3B was in adjacent *Salix aurita* carr with a pH range of 4.6–5.1. The fauna was impoverished relative to 3A but had *Vitrea crystallina*. *Vertigo lilljeborgi* was swept from submerged terrestrial vegetation at the west end of the lake, but was not encountered in the study plots. This is only the second recorded occurrence in W. Cork, the previous being from Lough Allua (Stelfox, 1929).

To find similar published faunal descriptions it is necessary to go to the Scandinavian literature. It is interesting to compare fens in the vicinity of Stockholm described by Waldén (1955) with these Irish sites. The effect of a drier climate is apparent. The most abundant shelled molluscs of base poor habitats in western Ireland are *Nesovitrea hammonis*, *Euconulus fulvus*, *Columella aspera* and *Punctum pygmaeum*, just like the situation in S.W. Sweden (Waldén, 1969).

It is impossible to draw sweeping conclusions from the description of conditions at only three sites. Much more quantitative work is needed to build up the detailed picture, but these glimpses are exciting. Mesotrophic vegetation can apparently yield considerable molluscan faunas.

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A REDISCOVERY OF *POTAMOPYRGUS*
CILIATUS (GOULD)
(GASTROPODA: HYDROBIIDAE)

B. VERDCOURT

Spring Cottage, Kimbers Lane, Maidenhead, Berks.

(Read before the Society, 15 November 1975)

Abstract: Details of a fortuitous collection of specimens of *Potamopyrgus ciliatus* (Gould) on the roots of a plant sent to Kew from Cameroun for identification are reported together with additional records from Ghana, Zaire and the Ivory Coast.

A young colleague Miss G. S. Lee brought along to me some shells she had noticed mixed with the roots of a plant in a collection sent to the Royal Botanic Gardens, Kew for naming. I recognized these as *Potamopyrgus ciliatus* (Gould) which is figured by Pilsbry and Bequaert (1927, fig. 21). These authors commented that the species had not been refound since its initial discovery in Liberia over 75 years previously. In fact they seriously suggested the possibility of an error of labelling, since Gould's species is virtually indistinguishable from a New Zealand species, *P. salleana* (Fischer). The specimens noticed by Miss Lee were attached to the roots of the Onagraceous plant, *Ludwigia adscendens* (L.) Hara subsp. *diffusa* (Forsk.) Raven (better known as *Jussiaea repens* L. var. *diffusa* (Forsk.) Brenan), a well-known water plant which floats by means of white to pink inflated spongy roots produced at the nodes, or more usually is found on muddy margins where it is affixed by more normal much divided fibrous roots. The plant was collected on 3 February 1974 by Dr. R. Letouzey as his number 12882. The data attached to this number are—Cameroun: banks of R. Nyong between Ndogtima Nyong and R. Dikobe, 15 km. NE. of the mouth of the R. Nyong. This is a considerable extension of range from the original type locality which is 'Liberia, Deea (Gbea or Mano) R., on the muddy margins'. At my request Dr. R. Letouzey examined the Paris material of his number 12882 and sent me a further 6 specimens. This has enabled me to send material to the British Museum (Nat. Hist.), London; Muséum d'Histoire naturelle, Geneva; Danish Bilharziasis Laboratory, Charlottenlund and the Musée de l'Afrique Centrale, Tervuren.

Dr. E. Binder, who has a detailed knowledge of West African freshwater molluscs, informs me that both he and M. Daget of Paris have found fresh material of the species in the Ivory Coast and that an anatomical study will eventually be published. Dr. David Brown has also recently found *P. ciliatus* in mangrove swamps in Ghana and drew attention to Moll's (1939) record of *P. ciliatus* (reported by Bequaert and Clench (1941)) from the Congo Estuary between Malela and Banana where it was found in the burrows made by shipworms (*Teredo*) in the live aerial roots of mangroves.

The species is clearly widespread on the West African coast and has been overlooked due to its habit of lurking in muddy places, its spines becoming covered, thus rendering

it difficult to see. References to the species can be summarized as follows:—

- 1850 *Amnicola ciliata* Gould: 196.
- 1927 *Potamopyrgus ciliatus* (Gould), Pilsbry and Bequaert: 222, fig. 21.
- 1939 *Potamopyrgus ciliatus* (Gould), Moll: 373.
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TRAPANIA MACULATA HAEFELFINGER, A DORIDACEAN NUDIBRANCH NEW TO THE BRITISH FAUNA

GREGORY H. BROWN AND BERNARD E. PICTON

Zoology Department, Bristol University

(Read before the Society, 17 May 1975)

Abstract: *Trapania maculata*, a rare Mediterranean dorid nudibranch, is recorded from Portland, Dorset. It is distinguished from the only other British *Trapania*, *T. pallida*, by its coloration.

Three specimens of an unusual phanerobranch dorid were found on 1 May 1974 in West Bay, Portland, Dorset, at 12m depth (10m below low water spring tides, LWST). The substratum was a large boulder embedded in the sandy sea bed. The rock provided attachment for abundant growths of polyzoans, *Chartella papyracea* and *Bugula turbinata*, together with *Scrupocellaria* sp. to which the animals were attached. These doridaceans proved to be the first British records of *Trapania maculata* Haefelfinger 1960, recorded previously only from the Mediterranean Sea.

DESCRIPTION

External features. The living animals measured 15-17 mm when extended. This species can be distinguished immediately from the only other representative of the genus found in British waters, *Trapania pallida* Kress, 1968, by its coloration. The body was pellucid white although the opaque gonads were visible internally. Yellow to orange pigment spreads over the head from the oral tentacles to form a patch tapering to a line passing between the rhinophores (Fig. 1). A triangular patch was situated just anterior to the gill circlet and may be flanked on either side by a spot. Posterior to the gills a mid-dorsal line broadens to cover the metapodium. The protective papillae lateral to the rhinophores and gills were also yellow/orange but longer and more slender than the equivalent papillae of *T. pallida* collected at Lundy Island in the Bristol Channel in July 1974.

Haefelfinger (1960) described an interrupted lateral line of pigment on either side of the animal but there was no indication of this in any of our specimens (Fig. 2E). He shows, furthermore, that the pigmentation may spread so that the patches anterior to the gills, on the anal cerata and on the head may be united.

The non-retractile rhinophores bore 8-9 lamellae (Figs. 2B, C and D); the lamellate clubs were yellow. There were three tripinnate gills around the anal papilla in all specimens. The median gill was the largest but all three were tipped with yellow. The foot, bearing distinct propodial tentacles, was narrow with a groove apparent along the mid-line (Fig. 2A). The animals were observed to attach more firmly to thin polyzoan stems than to a flat surface.

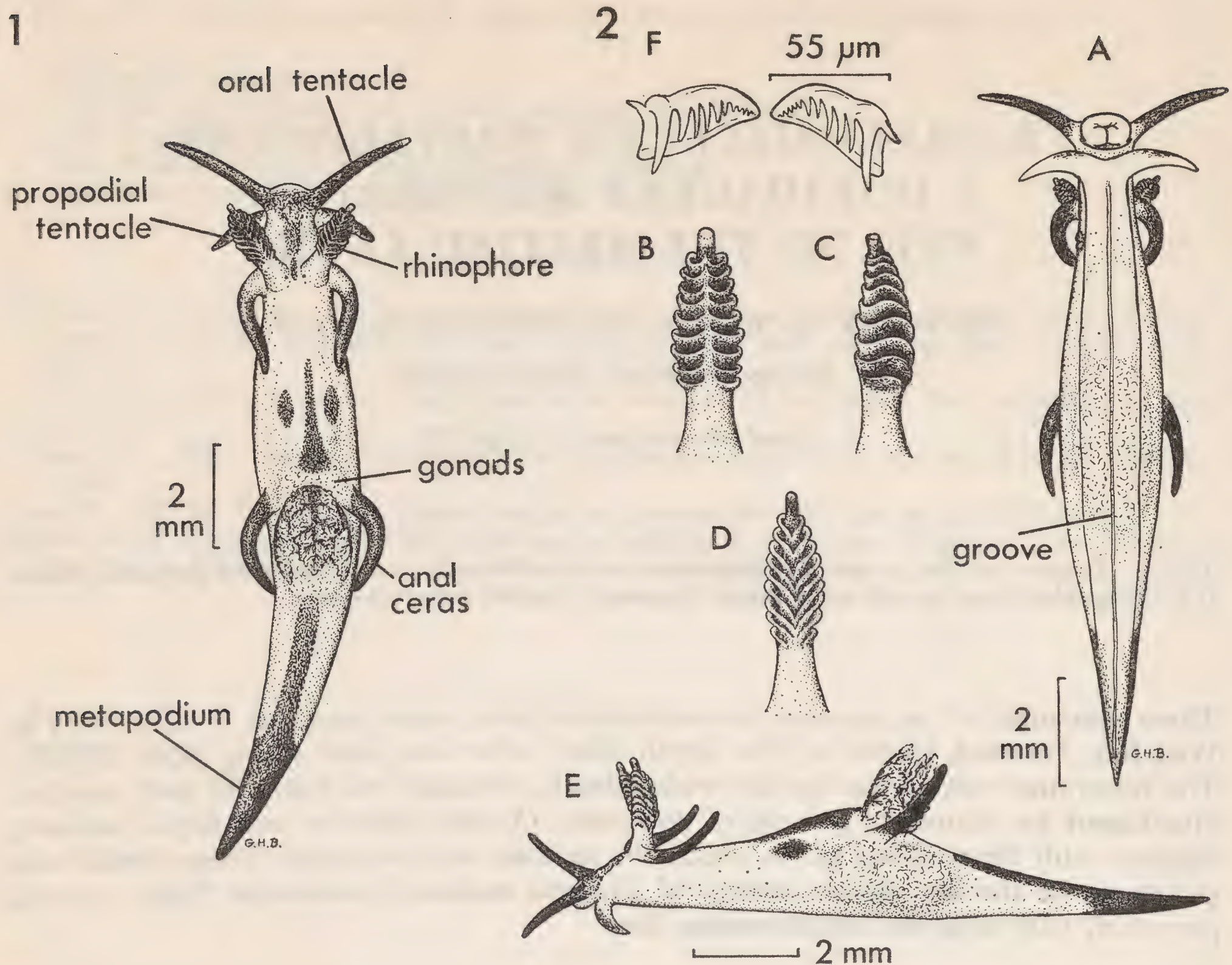


Fig. 1. *Trapania maculata* from the dorsal aspect. Fig. 2. A, ventral view. B, C and D, rhinophore; anterior, lateral and posterior views respectively. E, lateral view of whole animal. F, 22nd row of radula.

Anatomy. The radula in a 17 mm specimen was found to have the formula $1.0.1 \times 47$. This is considerably longer than the radula described by Haefelfinger 1960, for a 15 mm specimen. The teeth are serrated, the largest having an appearance similar to that shown in Fig. 2F. The penis was armed with numerous simple hooks. The spicules are simple as in the other members of the genus.

DISCUSSION

This species was first described by Haefelfinger in 1960 following collections at Villefranche-sur-Mer, on the Mediterranean coast of France. There are no previous records from the Atlantic although one other member of the genus, *Trapania pallida*, has been recorded from Britain (Kress 1968) and from Roscoff in the Bay of Biscay (Kress 1970). A further specimen of *T. pallida* was collected on 6 July 1974 from Lundy Island enabling a comparison of the living animals of both British species of *Trapania*. Although closely related, there can be no doubt that the species are distinct. Kress (1968) lists the eight known species of *Trapania* and the genus is shown to be widely dispersed with members from Japan, Brazil, California, the Mediterranean and Britain.

The authors wish to thank Dr. T. E. Thompson for help in preparing this manuscript.

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- , 1970. A new record of *Trapania pallida* (Opisthobranchia, Gastropoda) with a description of its reproductive system and a comparison with *T. fusca*. *Proc. malac. Soc. Lond.* **39**: 111-116.

REVIEW

The shell makers. Introducing molluscs. By Alan Solem. xii+289 pp., 12 colour plates, text illustrated. John Wiley and Sons, New York, London, Sydney, Toronto. Price £5.05.

This is an excellent book. The author demonstrates abundantly that molluscs are even more fascinating than their shells are beautiful and deserve at least as much attention. The general approaches of the book are evolutionary and functional. Text and illustrations (particularly the scanning electron micrographs) reveal many interesting details (often new) about the diversity and morphology of molluscs.

The book divides into three broad sections. Chapters 1–3 introduce the subject, outline the diversity and fossil history of molluscs, and discuss their position in the classification of living things. Chapters 4–7 describe the main molluscan classes in more detail, while chapters 8–13 deal with distribution, functional morphology and evolution. In these last chapters Solem brings his wide knowledge to bear best and they are the book's major strength. Four appendices summarize the classification of taxa mentioned in the text, list major references to molluscs, provide a glossary of technical terms, and give hints on the care of living molluscs. The reader whose enthusiasm is aroused can thereby further his interest. Finally an adequate index finishes the book.

'The shell makers' starts slowly. Chapter 1 covers several seemingly unrelated topics and uses imperial measures. I am unimpressed to learn that snails range in size from $1/37$ to $27\frac{3}{4}$ inches! Chapters 2 and 3 improve, although some will find the classification of life into five kingdoms and Solem's idea of the archetypal mollusc, novel. However the reasoning behind both is clearly explained. Chitons, cephalopods and bivalves are described efficiently. Two chapters are devoted to gastropods and include a new hypothesis on the origin of torsion as well as a discussion of their multifarious modes of feeding.

Chapter 8 treats freshwater molluscs and paints a depressing picture of their future, particularly in N. America. Chapter 9 discusses the functional morphology of the radula, is crammed with new facts and ideas, and excellently illustrated with SEM photos of radula teeth. No one can doubt the wear on radula teeth after seeing figs. 1b and 1f in chapter 9. Other figures reveal the fascinating way each tooth is forced into position by its predecessor as the radula rotates in the feeding motion, and the amazing diversity of tooth form in snails' radulae. Within this chapter are 12 colour plates which illustrate far more live molluscs than dead shells, however beautiful. Incidentally they reveal that the inhabitants are often even more colourful than the shells.

The evolution of terrestrial gastropods and the problems of life on land are discussed next, followed by an account of the functional morphology of shells again illustrated with SEM photos. The spines and laths shown in figs. 4 and 5 (Chapter II) elucidate how constricted apertures in land snails function to protect them from predators, a topic that has puzzled me for several years. Chapter 12 deals with slugs and produces a realistic hypothesis on why and how they evolved from snails, apparently abandoning the protection of their shells. Finally chapter 13 summarizes distribution patterns of molluscs today.

The style is easy and the layout pleasing. Two factual errors (a mantle is not unique to molluscs, brachiopods have one (p. 15); epiphragms do not significantly reduce water loss (p. 181)); the half dozen misprints, and occasional americanisms (sowbug (p. 51)); 'a liter is slightly more than a quart' (p. 72); Australian repeatedly for Australasian; spire angle for spiral angle) do not detract from the general excellence although one or two of the latter jar somewhat. 'Self-amputate' (p. 215) and 'look-alikes' (p. 233) may be more readily understood than autotomise or homeomorphs but 'to predate' for 'to prey' (p. 55) is definitely not acceptable. The illustrations are excellent but have been numbered in an unusual way which makes cross reference between chapters cumbersome. Keeping up a long printing tradition, the publishers have reversed the photograph on the dust jacket which shows abundant sinistral *Polymita picta*!

All in all a fascinating, well illustrated book, full of a wealth of new facts and ideas to stimulate further observation and research on molluscs. There is something here for amateur and professional and the price puts the book well within reach of both. I whole-heartedly recommend it.

C.R.C.P.

OBITUARY

ARTHUR BLOK, 1882-1974

Arthur Blok was born in Stoke Newington, London on 20 March 1882 and was educated at Owens School (The Brewers Company) and University College, London in the Faculty of Electrical Engineering where he obtained the degree of B.Sc., becoming personal assistant to Prof. Sir Ambrose Flemming.

Most of Blok's working life was spent in the Civil Service, in the Ministry of Munitions and Board of Trade 1916-1920 and at the Patent Office, from where he retired as Principal Examiner in 1942. From 1942 to 1947 he served in the Department of Scientific and Industrial Research and the Ministry of Supply, both on atomic energy. He semi-retired to Rottingdean, Brighton, Sussex, in January 1948 as consultant to the Ministry of Supply, Department of Atomic Energy. He finally retired from the Civil Service in December 1954. The O.B.E. was bestowed on him in 1945.

Amongst his other activities Arthur Blok acted as the first Principal of the Haifa Technion and remained a member of its Board of Governors until his death. He was awarded an honorary D.Sc. by the Technion in 1972. He was also for a time head of the Evening Department of Electrical Engineering, Croydon Polytechnic and lecturer in Electrical Engineering at Queen Mary College, University of London. In 1948 he delivered the Ambrose Fleming Memorial Lecture at the Royal Institution. He acted as consultant on electrical work at the first hydro-electric power station on the River Jordan and for the first Dead Sea potash plant. He was a past president of the Brighton Natural History Society and vice Chairman of the Rottingdean Preservation Society.

One of Arthur's particular interests was in problems concerned with electric lighting and he was an associate member of the Institution of Electrical Engineers and a member of the Council of the Illuminating Engineering Society. He took an active part in the discovery and development of wireless and the application of atomic energy. He made some of the equipment used in the transmission of the first radio messages. He was present at Poldhu, Cornwall in 1902 when the first radio signals were transmitted across the Atlantic to the inventor Marconi, in Newfoundland. He once told the writer that he felt that he had been extremely fortunate in having played a part, even though a micro-one, in two developments which have changed the face of the world. The most unassuming of men, he always tended to play down the part he had taken in these world-shattering discoveries.

A member of the Conchological Society of Great Britain and Ireland since 1924, he was made an honorary member in 1972. He joined the Malacological Society in 1930. In 1925 he represented Great Britain at the *Réunion amicale des Malacologistes et Paléontologistes*. His rôle of promoting concord between the two British Societies continued to the last, in January 1967 he made the speech of welcome to the joint meeting of the Conchological and Malacological Societies.

Conchology was for him a recreation. He acquired most of his shells between the wars by attending the well known natural history sales at Stevens Auction Rooms in Covent Garden, and in this way built up his very large collection which he kept in immaculate order. Indeed, an almost obsessive interest in order and neatness characterized all Blok's activities. He contributed very little to conchological literature and had no interest in field work, but as a curator he surely had no peer. He often said that he had never regretted following the advice of J. R. le B. Tomlin not to become a specialist. His consequently wide knowledge of all shell groups was at the disposal of anyone interested in them, so collectors often turned to him for advice when they had a knotty identification problem or wanted to know about some obscure aspect of conchology.

His curiosity led Blok to investigate many conchological by-ways. He traced a descendent of Ronca, one of the late Victorian cameo-cutters, obtained his surviving tools and assembled material for an illustrated lecture, delivered to the Conchological Society in June 1937. The structure of shells was another of these interests. He gave a lecture on this subject to the London Branch of the Conchological Society in April 1932. His interest in the use of shells as money and as ornaments gave rise to a talk at the Jubilee meeting of the Malacological Society on the 28 February 1943. His talk, *Shells and ornament* was illustrated by examples of shell girdles, brooches, buttons, cameos, card cases, spoons, snuff boxes and others from his own collection.

His library, like his collection extensive and very general, consisted of some 600 molluscan books and upwards of 3,000 offprints. Both his library and collection were presented to the Hebrew University of Jerusalem during his lifetime and he supervised the packing, unpacking and its installation in Jerusalem. His library also contained a series of some 470 conchologists holograph letters, one of the largest in the United Kingdom, which he always considered very useful in the identification of collections and collectors labels. This is now in the possession of Mr. S. P. Dance.

Arthur Blok's most important contributions to conchology were his ability to interest and inspire others in the science, and in his beautifully curated collection and library which provided a nearly infallible reference tool for any who cared to call and make use of it.

LIST OF PUBLICATIONS BY A. BLOK

- 1943 Shells and ornament. *Proc. malac. Soc.* **25**; 136-137.
1948 The shell collection of the late Rev. E. G. Alderson with special reference to the genus *Pila*. *J. Conch., Lond.* **22**; 299-302. (With T. Pain.)
1950 Pearl in *Tellina*. *J. Conch., Lond.* **23**: 98.
1968 The care of the collection. *Conch. Soc. Papers for Students No. 10.* (with T. E. Crowley.)
Non-conchological
1914 *The elementary principles of illumination and artificial lighting.* Scott Greenwood, London.

T. Pain

INSTRUCTIONS TO AUTHORS

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e.g.

ELLIS, A. E. 1926. *British snails. A guide to the non-marine Gastropoda of Great Britain and Ireland, Pliocene to Recent.* 275 pp., 14 pls., Oxford.

BROWN, P. and STRATTON, G. B. (Editors). 1965. *World list of scientific periodicals published in the years 1900–1960.* (4th Ed.) 3 vols. London.

For periodicals give full title of the article, title of the periodical abbreviated according to the World List (4th Ed.), volume number, page numbers and plates.

e.g.

WOODWARD, F. R. 1965. Monograph of the British Lower Tertiary Unionidae, with descriptions of three new species. *J. Conch., Lond.* **25**: 316–330, pls. 22–27.

GOULD, S. J. 1969. An evolutionary microcosm: Pleistocene and Recent history of the land snail *P. (Poecilozonites)* in Bermuda. *Bull. Mus. comp. Zool. Harv.* **138**: 407–532, 5 pls.

8. Authors may obtain copies of all papers (other than brief notes) at cost price if ordered from printers (address: Messrs. Willmer Brothers Ltd., 62–68 Chester Street, Birkenhead, England) when galley proofs are returned.

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OBSERVATIONS ON THE BREEDING HABITS OF *OPEAS GRACILE* (HUTTON) (GASTROPODA: SUBULINIDAE)

SWAPAN KUMAR BISWAS, REZAUR RAHMAN AND TRIDIB RANJAN MITRA

Ecology Division, Zoological Survey of India, Calcutta

(Read before the Society, 21 February 1976)

Abstract In the field *Opeas gracile* aestivates for half the year, becomes active a few days before the monsoon rains, feeds for two days and then mates and deposits eggs. In the laboratory individuals do not aestivate and produce more than one clutch of 1-14 eggs per year. Freshly hatched young reared in isolation matured in as little as 13 weeks and produced viable eggs which hatched after 10 days.

Opeas gracile (Hutton) is a common garden snail in Calcutta. It remains active for a short period each year during the rainy months. Thus, for about half or little more than half of the year it is totally inactive. An interesting feature of the biology of this snail is that it does not aestivate in the laboratory. Pilsbry and Bequaert (1927) reported its cosmopolitan distribution, Mitra and Biswas (1974) recorded its necrophagous habits and Mitra *et al.* (1976) report its general feeding habits. The present paper describes the breeding of this snail, based on observations in the field by one of us (T.R.M.) since 1969 and in the laboratory.

Pulmonates are in general simultaneous hermaphrodites (Hyman 1967). Some authors, e.g. Meer Mohr (1949), Rensch (1955) have described mating in *Achatina fulica*, while Meissenheimer (1907) gave an account, in great detail, of the mating behaviour of *Helix pomatia*. Ghosh (1959) demonstrated that mating is not essential for oviposition in *Achatina fulica* and *Macrochlamys indica*. In this context our observations on the breeding habit of *Opeas gracile*, both in field and laboratory, appear worth reporting.

OBSERVATIONS

In the field. After a long period of aestivation the snails, some with and some without eggs awake to a normal animated condition a few days before the monsoon arrives. For a couple of days they remain busy feeding and then become restless and start laying eggs. Oviposition usually occurs at night in humid soil or under fallen leaves. Even among ovigerous individuals, mating occurs regularly both at night and in the day.

In the laboratory. It was possible to study breeding in some detail. Large numbers of specimens, both adult and juveniles, were kept in glass jars, with soil from their normal habitat moistened in the rain water. They were provided with fallen etiolated (yellow) leaves of *Clitorea ternatea* as food.

Individuals ripe for copulation, crawl about with seeking movements, sometimes pausing with the anterior part of the body lifted. When two such individuals come across one another they test each other with their tentacles and then erect the anterior parts of the body, while pressing the foot firmly on the substrate. Meanwhile they continue to make contact with the tentacles and oral lappets. After a pause of about three to five

minutes, the caresses are resumed. Tonic body contractions, ending in strong convulsions then ensue. Egg laying, usually occurs during the night. In one instance one of us (S.K.B.) observed it in the day time. There is no fixed place for egg laying, although isolated individuals usually lay under soil. In heavily populated jars, eggs are laid sometimes on the walls and lids of the jars. The number of eggs per clutch varies from 1 to 14. These are laid one after another, sometimes in a circle. The number of clutches per individuals per year is variable; it is usually more than one.

The eggs are rounded, and covered with a thick, tough, calcareous shell, white in colour and not easily breakable. The diameter of the eggs varies from 0.9 to 1.10 mm. They contain developing embryos. Once laid, the eggs are not cared for by the parents although they are sometimes found to wait near them for a few minutes. This probably permits recovery from the exhaustion of egg laying, as in the case of *Achatina fulica* and *Macrochlamys indica* (Ghosh 1959).

Hatching was observed in the daytime by one of us (T.R.M.) when the young individuals, bathed in mucus, broke through the shell. Freshly hatched snails become active soon after birth and are negatively geotactic. They crawl up the walls of their containers before commencing to feed.

Self fertilization. To ascertain whether cross fertilization is essential in the oviposition of the snail, several newly hatched individuals were separated and reared with special care. One individual was found to attain sexual maturity after 13 weeks and laid eggs which hatched out on the 10th day after laying. Others were found to lay their eggs in the winter months, i.e. from November to February, from which hatching of young individuals was also visible. Isolation of the young from an earliest age rules out the possibility of fertilization by sperms received in the previous year.

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TWO POSTGLACIAL MOLLUSCAN FAUNAS FROM SOUTH-WEST ENGLAND

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(Read before the Society, 21 February 1976)

Abstract: Two Postglacial non-marine molluscan assemblages from S.W. England containing the locally extinct species *Spermodea lamellata* are described. It is suggested that both belong to the deciduous forest optimum of the Flandrian (c. 7500—c. 5000 B.P.).

The purpose of this brief paper is to put on record two Flandrian (Postglacial) non-marine faunas from S.W. England, both containing *Spermodea lamellata* (Jeffreys), a species not otherwise known from that part of the British Isles, living or fossil.

1) *Tornewton Cave, Torbryan, South Devon (SX 817673)*. An account of the complex stratigraphy of Tornewton Cave has been published by Sutcliffe and Zeuner (1962). In April 1958, through the courtesy of Dr. A. J. Sutcliffe, I visited the excavations. The only horizon within the cave to yield Mollusca was the relatively late Layer D ('Widger's Diluvium'). This layer had mostly been removed during excavation in the 1870's, but a small portion remained adhering to the wall of the 'Middle Tunnel', underlying a thin surface layer of hard stalagmite (Sutcliffe and Zeuner, plate 28). The material is an indurated tufaceous loam containing angular fragments of limestone and heavily cemented by secondary calcite. Small vertebrate remains are common, scales of the slow-worm (*Anguis fragilis* L.) being notably abundant. A 2 kg sample yielded the Mollusca listed in Table 1.

Some of the snails, especially the abundant *Oxychilus cellarius*, may have lived within the cave, but most were probably washed in and reflect the environment on the slopes above the entrances. The assemblage is that of forest. There is a total absence of the open-ground genera *Pupilla*, *Vallonia* or *Helicella*. Habitats for the rock-loving *Pyramidula rupestris* were evidently provided by bare limestone surfaces.

Zenobiella subrufescens is represented by a damaged shell 3.7 mm in diameter and a few small fragments. This is the first fossil record of this woodland snail in the British Isles. The delicacy and feeble calcification of the shell may partly be responsible for this; also relatively few deposits have been studied in western areas where the species mostly occurs. Further examples have recently been detected in a Flandrian deposit at Nash Point, Glamorgan (J. G. Evans, unpublished).

The Tornewton site remains covered by deciduous woodland. A careful search in 1958 and again in 1974 revealed the living presence of all the terrestrial species found in Layer D with the exception of *Vertigo pusilla*, *Leiostyla anglica*, *Spermodea lamellata*, *Columella edentula*, *Nesovitrea hammonis* and *Zenobiella subrufescens*. The first three of these species are not known to occur living in South Devon (vice county 3).

2) *Blue Anchor Bay, near Minehead, Somerset (ST 022438)*. A sample from this site, collected by Miss J. Waddle, was forwarded to me by Mr. J. N. Carreck (Queen Mary College,

University of London) in 1958. The deposit can still be seen (1975) exposed between tide marks on the foreshore, directly below the railway station at Blue Anchor. The material is a black organic detritus mud with compressed wood fragments and with intercalations of paler calcareous silt. In places it is overlain by a thin layer of pure wood peat. The 1958 sample (about 1.5 kg) yielded the Mollusca listed in Table 1, below:

TABLE 1

	Tornewton	Blue Anchor Bay
<i>Valvata cristata</i> Müller	—	1
<i>Valvata piscinalis</i> (Müller)	1	—
<i>Acicula fusca</i> (Montagu)	1	—
<i>Carychium minimum</i> Müller	—	709
<i>Carychium tridentatum</i> (Risso)	14	747
<i>Aplexa hypnorum</i> (Linné)	—	15
<i>Lymnaea truncatula</i> (Müller)	—	27
<i>Anisus leucostoma</i> (Millet)	—	131
cf. <i>Oxyloma pfeifferi</i> (Rossmässler)	—	5
<i>Cochlicopa lubrica</i> (Müller)	1	7
<i>Cochlicopa lubricella</i> (Porro)	6	2
<i>Cochlicopa</i> sp.	10	8
<i>Pyramidula rupestris</i> (Draparnaud)	10	—
<i>Columella edentula</i> (Draparnaud)	5	8
<i>Vertigo pusilla</i> Müller	5	16
<i>Leiostyla anglica</i> (Wood)	7	13
<i>Lauria cylindracea</i> (da Costa)	45	30
<i>Acanthinula aculeata</i> (Müller)	5	3
<i>Spermodea lamellata</i> (Jeffreys)	1	51
<i>Ena obscura</i> (Müller)	1	1
<i>Punctum pygmaeum</i> (Draparnaud)	3	20
<i>Discus rotundatus</i> (Müller)	17	252
<i>Vitrina pellucida</i> (Müller)	3	—
<i>Vitrea crystallina</i> (Müller)	2	15
<i>Vitrea contracta</i> (Westerlund)	21	15
<i>Nesovitrea hammonis</i> (Ström)	1	5
<i>Aegopinella pura</i> (Alder)	23	13
<i>Aegopinella nitidula</i> (Draparnaud)	21	256
<i>Oxychilus cellarius</i> (Müller)	111	29
<i>Oxychilus alliarius</i> (Miller)	10	5
<i>Zonitoides excavatus</i> (Alder)	—	2
<i>Zonitoides nitidus</i> (Müller)	—	7
<i>Deroceras</i> sp.	—	33
<i>Euconulus fulvus</i> (Müller)	4	10
<i>Clausilia bidentata</i> (Ström)	2	11
<i>Balea perversa</i> (Linné)	—	5
<i>Monacha granulata</i> (Alder)	9	72
<i>Zenobiella subrufescens</i> (Miller)	2	—
<i>Trichia hispida</i> (Linné)	1	—
<i>Arianta arbustorum</i> (Linné)	2	1
<i>Cepaea nemoralis</i> (Linné)	1	4
<i>Cepaea hortensis</i> (Müller)	2	2
<i>Cepaea</i> sp.	—	3
<i>Pisidium personatum</i> Malm	—	421

The environment indicated is that of a shaded swamp with stagnant pools of water, probably fen woodland (alder carr). The presence of two examples of the calcifuge snail *Zonitoides excavatus*, a very rare Postglacial fossil, is specially noteworthy. Three species (*Vertigo pusilla*, *Leiostyla anglica*, *Spermodea lamellata*) are unknown living in Somerset.

KERNEY: TWO POSTGLACIAL MOLLUSCAN FAUNAS

A wood fragment (alder) associated with this sample was recently submitted to the Cambridge University Radiocarbon Dating Laboratory, with the following result: Q-1343 6730 ± 150 B.P.

Dr. C. Turner kindly examined part of the same sample for fossil pollen. Although the pollen proved to be somewhat corroded, he obtained the following spectrum:

<i>Betula</i>	2.0	Cyperaceae	6.5
<i>Pinus</i>	1.0	Compositae	+
<i>Ulmus</i>	1.5	Chenopodiaceae	1.0
<i>Quercus</i>	9.5	Rosaceae	+
<i>Tilia cordata</i>	1.0	<i>Myriophyllum spicatum</i>	0.5
<i>Alnus</i>	56.0	<i>Sparganium</i> type	0.5
<i>Corylus</i>	12.5	<i>Polypodium</i>	2.5
<i>Hedera</i>	3.5	<i>Pteridium</i>	3.0
Gramineae	5.0	Filicales	3.0

(Figures are for percentages of total identifiable land pollen based on a count of 250 grains; corroded, degraded and crumpled grains account additionally for a further 23%).

Dr. Turner regards this spectrum as diagnostic of pollen zone VII, most probably zone VIIa (Atlantic period, *ca.* 7200–*ca.* 5000 B.P.), an interpretation fully in agreement with the radiocarbon dating.

In spite of their differences in facies, the molluscan assemblages from Tornewton Cave and from Blue Anchor Bay show certain resemblances. Both represent closed forest. They are characterized by *Carychium tridentatum*, *Vertigo pusilla*, *Discus rotundatus*, *Aegopinella* spp., and *Oxychilus cellarius*, together with two species now almost extinct in southern England, *Leiostyla anglica* and *Spermodea lamellata*. The open-ground genera *Pupilla*, *Vallonia*, *Helicella* and *Trichia* are absent or virtually so. This association corresponds with molluscan assemblage zone d of Kerney and Turner (1977), as defined within a series of Flandrian deposits at Folkestone in Kent.

At Folkestone the base of zone d is dated by radiocarbon at 7500 ± 100 B.P. and has yielded a pollen spectrum diagnostic of pollen zone VIc (oak/elm/lime zone). More dates are needed, but provisionally it may be suggested that such a molluscan assemblage may prove to be distinctive of the deciduous forest optimum (pollen zones VIc–VIIa; late Boreal-Atlantic periods), over a considerable area of southern England.

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My thanks are due to Dr. Charles Turner for examining the pollen from Blue Anchor Bay, and for making possible the radiocarbon dating from this site.

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NON-MARINE MOLLUSCA FROM FAVERSHAM, KENT, FIGURED BY GEORGE WALKER IN 1784

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(Read before the Society, 21 February 1976)

Abstract: The identity of the species of non-marine Mollusca from the Faversham area figured in Walker's *Testacea Minuta Rariora* (1784) is discussed. Several represent the first known British records.

Very few local lists of non-marine Mollusca date from before the 19th century. One of the most interesting is contained in a now rare book by George Walker (1784), which deals largely with Foraminifera found by William Boys of Sandwich in shell-sand from the shore of Sandwich Bay, Kent. The importance attaching to these early descriptions of Foraminifera (Parker and Jones 1859) has tended to overshadow the fact that the book also describes non-marine Mollusca from the Faversham area. Walker, who was a book-seller in Faversham, tells us (p. iv): 'Being anxious of adding still more to this elegant collection, than the Sand from Sandwich had afforded, I have examined . . . the banks of fresh water streams and ditches, the boggy places, and the woods in this neighbourhood, whereby very considerable additions have been made, which are noticed in the explanatory index'. Walker drew the figures which appear on the three engraved plates, although the descriptions (the work is non-binomial) were provided by Edward Jacob (1710?-1788), a local botanist, perhaps best remembered today for his pioneer work on the fossil fruits of the London Clay of the Isle of Sheppey.

Walker's figured specimens are lost. They may well have been in the collection which he tells us (p. ii) he presented to the Duchess of Portland, and which was included in the Portland sale two years later (Anon, 1786, p. 139, item no. 3088: 'A curious collection of minute Shells from the English Coast, *including most of the new species figured by Walker . . .*'). A good many years afterwards William Boys and his son Henry sent further material to George Montagu, to help him establish the identity of Walker's species for *Testacea Britannica* (Montagu, 1803, xii; 1808, ii). This evidence is valuable, and, so far as the non-marine species are concerned, Montagu's determinations, in fact, mostly agree with those given in the list below. But it is clear from a reading of Montagu's text (1803, pp. 194, 339, 459) that the shells he saw were probably in all cases from the neighbourhood of Sandwich—not Faversham—being merely considered by the Boys's to be representative of those illustrated in Walker's drawings. One or two mistakes clearly crept in in this way, notably Montagu's misidentification of Walker's figure 21—evidently a specimen of *Acanthinula aculeata*—as *Helix nautilus* (= *Armiger crista*) (Montagu 1803, p. 465).

Though crudely drawn, most of Walker's Faversham shells are recognizable. They are as follows (an asterisk (*) indicates a first known British record):

Fig. 18. **Valvata cristata* Müller. 'In a fresh water Stream, near Faversham'.

Fig. 19. *Gyraulus albus* (Müller). 'From the same place as No. 18'.

Fig. 20. **Armiger crista* (Linné). 'From the same place as No. 18'.

Fig. 21. *Acanthinula aculeata* (Müller). 'From Bysing Wood, near Faversham—exceeding rare'.

- Fig. 23. *Vallonia* sp. (probably *V. pulchella* (Müller)). 'In marshy ground near Faversham—common'.
- Fig. 28. **Segmentina nitida* (Müller). 'From Hernhill Brooks on Flags—very rare'.
- Fig. 33. ?*Bithynia* sp. (possibly a juvenile *B. leachii* (Sheppard)). 'From Faversham Creek—not common'.
- Fig. 41. *Ena obscura* (Müller). 'From a ditch-bank near Faversham—not common'.
- Fig. 42. **Acicula fusca* (Montagu). 'From Bysing Wood, near Faversham—very rare'.
- Fig. 50. **Ovatella myosotis* (Draparnaud). 'On the roots of rushes in marshes near Faversham—very common'.
- Fig. 51. **Carychium* sp. (probably *C. tridentatum* (Risso)). 'In the mossy banks of a stream near Faversham—common'.
- Fig. 53. **Ovatella myosotis* (Draparnaud) (a juvenile shell). 'In moss of boggy ground near Faversham—not uncommon'.
- Fig. 54. *Aplexa hypnorum* (Linné). 'On the bank of a stream near Faversham—not uncommon'.
- Fig. 56. *Valvata piscinalis* (Müller). 'From Faversham Creek—not common'.
- Fig. 57. **Lymnaea truncatula* (Müller). 'From a stream near Faversham—very rare'.
- Fig. 59. **Cecilioides acicula* (Müller) (a juvenile shell). 'From Faversham Creek—very rare'.
- Fig. 60. **Cecilioides acicula* (Müller). 'From Faversham Creek—but not uncommon there' (this and the last were obviously dead shells found in flood rubbish).

A few comments are called for. Most of these species have been refound in the neighbourhood of Faversham in recent years (10-km grid squares TQ 95, 96, TR 05, 06). Of the three exceptions, two, *Aplexa hypnorum* and *Vallonia pulchella*, could no doubt be added by further search, although both are local in Kent and are probably scarcer than they were in the 18th century owing to the draining of suitable marshy ground. The third, *Segmentina nitida*, is however undoubtedly rare, and may be extinct hereabouts. The only other East Kent records of *S. nitida* are all from the area of the Stour marshes between Canterbury and the Isle of Thanet, and most of the localities have not been confirmed for many years. The exact site of Walker's find is a little uncertain. The immediate surroundings of the village of Hernhill (about 3½ miles east of Faversham) seem rather unpromising for this species, and the 'Brooks' are more likely to have been a mile or two to the north, on the landward edge of the coastal marshes around Graveney.

But the record of greatest interest, and the only one to raise a possible taxonomic problem, is the *Acicula* (figure 42). Montagu (1803, p. 330) founded his new species of *Turbo fuscus* (= *Acicula fusca* (Montagu)) on this rather rough illustration and the accompanying very brief description (he expressly says that he saw no specimen), and Bysing Wood must therefore be regarded as the type locality. Watson (1943, p. 15) agreed that the figure represented an *Acicula*, but pointed out that there is a slight possibility that more than one species of *Acicula* might occur in the south of England (e.g., the continental *A. lineata* (Draparnaud)) and he therefore urged that topotype material of *fuscus* should be collected. For this specific purpose the Conchological Society held a field-meeting at Faversham on 2 May 1965. Bysing Wood lies about a mile west of the town (NGR TQ 9962) and consists largely of old hornbeam coppice with patches of *Mercurialis*. We failed to find *Acicula* here, although the discovery at TQ 995618 of living *Phenacolimax major* (Férussac) (still the only known site in vice-county 15) tends to confirm that the wood is ancient. Later on in the same day several living *Acicula* were, however, found in a hazel coppice rather over a mile further south (TQ 985603). These were all quite typical of our well-known British form, and help to establish the identity of Montagu's *Turbo fuscus* beyond reasonable doubt.

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REVIEW

Pulmonates. Volume I. Functional Anatomy and Physiology. Edited by Vera Fretter and J. Peake. Academic Press. 1975. 417 pp. Price £17.50.

This, the first of two volumes of review articles on the pulmonates, concentrates on the functional anatomy and physiology. The second volume, when published, will cover systematics, evolution and ecology. Volume I opens with a chapter by Dr. Fretter which introduces the pulmonate molluscs as essentially land and fresh-water animals and outlines the position of the sub-class Pulmonata within the class Gastropoda. Dr. Fretter then gives a broad view of the adaptive radiation shown by the structure and function of the pulmonate body, and this account is illustrated by specific examples. Pulmonates are then compared with the sub-class Opisthobranchia (sea-slugs etc.) and a concluding discussion follows on the interpretation of body structure in terms of the origin and evolution of the sub-class Pulmonata (slugs and snails).

The main section of the book consists of eight chapters, each written by a different specialist author. These include: Locomotion by H. D. Jones; Respiration by F. Ghiretti and A. Ghiretti-Magaldi; Alimentary canal by N. W. Runham; Water relationships by J. Machin; Nervous system, eye and statocyst by G. A. Kerkut and R. J. Walker; Endocrinology by H. H. Boer and J. Joosse; Reproduction by C. J. Duncan and Development by C. P. Raven. One obvious omission is the structure of the kidney, which is not included in the chapter on water relations, although urine formation is described. Each chapter is a complete entity and is supplied with a long list of references: these are of especial value to the research student in enabling him or her to locate the original source of publications which are summarized or discussed in the text. However the omission of the titles of papers in the references is tantalizing, especially as the reference lists are such an important feature of this book. Some difference in style and detail of content is to be expected in any volume where each chapter is contributed by a different author. All of the chapters are illustrated by figures, tables or photographs and there is both a systematic and subject index at the end of the book.

In reading the various chapters, one becomes aware of the limited range of examples of the genera and species quoted: a few convenient laboratory species, which are comparatively large and easy to keep and breed in captivity, feature in almost every chapter. In some cases the limited range of species reflects the personal research bias of the author, while in others it reflects our very limited knowledge of the biology of this group of molluscs. The study of pulmonates is an international one, but a glance at the examples listed shows a strong European bias: there are obviously many interesting slugs and snails from other areas, often where the habitats are threatened, which await further study. This book should therefore serve both as a summary of existing knowledge and as a stimulus for further research on a different selection of genera and species.

The format and approach of this volume is similar to that of the two volumes on 'Physiology of Mollusca' (1964 and 1966) edited by K. M. Wilbur and C. M. Yonge, also published by Academic Press, and several of the chapter headings are the same. However, Wilbur and Yonge cover the whole of the Mollusca, and references to the Pulmonata are often brief. The new book by Fretter and Peake adds to this, and also includes many of the new publications on pulmonates which have appeared in the last ten years.

J. E. CHATFIELD

ON THE STATUS OF *MUREX OSSEUS* REEVE, 1845 (GASTROPODA: MURICIDAE)

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Abstract: Comparison of the holotype of *Murex osseus* Reeve, 1845 with specimens, and recently published figures of the lectotype, of *Pterynotus* (*Purpurellus*) *pinniger* (Broderip, 1832) indicates that the two are synonymous. The latter is the oldest available name.

There has been much speculation in the past, regarding the status of the taxon described by Reeve (1845, pl. 14, fig. 60) as *Murex osseus*. There is, however, no doubt that this species was correctly referred to the genus *Purpurellus* Jousseaume, 1880 by Vokes (1971, p. 77) which Emerson and D'Attilio (1969) regard as a subgenus of *Pterynotus* Swainson, 1833.

The statement by Vokes (1971, p. 77) that Reeve's *osseus* came from West Africa, appears to be without foundation. The type and only known specimen from the collection of Miss Saul, now in the Zoology Museum of the University of Cambridge, is without locality, as are all the Saul Muricinae (see Bishop 1976, p. 43). Reeve (1845) gave no locality, neither did Sowerby (1879, pl. 10, fig. 91). Tryon (1880, p. 87) stated habitat unknown, but went on to say, '*Murex gambiensis* Reeve, from the mouth of the Gambia, West Coast of Africa, is evidently the same species and I suspect that *M. uncinarius* Lamarck, from the Cape of Good Hope, will prove to be the young; I find no other differences than size between them'. One can only conclude that this author had never seen specimens of *Poroptychus uncinarius* (Lam.). Tryon's statement that *Pterynotus* (*Purpurellus*) *osseus* and *P. (P.) gambiensis* are conspecific may well be responsible for subsequent references to *P. (P.) osseus* as being from West Africa and possibly identical with '*M. gambiensis*'. Nicklès (1950, p. 90) evidently accepted this, since he makes '*M. gambiensis*' a synonym of '*M. osseus*'. Both species were, however, described in the same year, 1845.

Reeve (1845) said of '*M. osseus*', 'The *Murex pinniger* is perhaps the nearest allied species to this, though of very different form'. Tryon (1880, p. 112) discussing *P. (P.) pinniger* (Broderip, 1833) said, 'Has very close analogies with "*M. osseus* Rve. and is so like the young of that species ("*M. gambiensis*") that were it not for the wide difference of locality, I would scarcely hesitate to put them together". However, since the type of '*M. osseus*' is without locality this particular point does not arise.

Through the kindness of Dr. M. J. Bishop I have been able to examine Reeve's type of '*M. osseus*' and compare this shell with specimens of both '*M. gambiensis*' Reeve and '*M. pinniger*' Broderip. It is purplish white in colour, stained with chestnut brown, especially along the base of the last varix. There is a strong node between each of the three varices, the edges of which form wavy foliations as in the lectotype of *P. (P.) pinniger* figured by Emerson (1960), which it strongly resembles. In both the types of *P. (P.) osseus* and *P. (P.) pinniger* the foliations are shorter, more delicate and less digitate than in the West African species *P. (P.) gambiensis* and the up-curved protuberances on the shoulders of the whorls are much shorter. A specimen of *P. (P.) pinniger* from Guaymas,

Sonora, Mexico, in the author's collection, with which Reeve's type of '*M*'. *osseus* was compared, proved almost identical both in form and colour, but was smaller, length 60.5 mm. max. diam. 29.5 mm. The type of '*M*'. *osseus* measures length 74.5 mm. max. diam. 33.0 mm. In view of the fact that all available evidence points to a close relationship between them, it is concluded that *P. (P.) osseus* (Reeve 1845) should be relegated to the synonymy of *P. (P.) pinniger* (Broderip, 1833).

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ABIDA SECALE (DRAPARNAUD) (GASTROPODA: CHONDRINIDAE) IN NORTH-WEST ENGLAND

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AND

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Abstract: A survey of Pennine sites apparently suitable for *Abida secale* in August 1974 revealed that *A. secale* is almost completely restricted to sites west of the Pennine watershed. Sites were categorized as (a) open, (b) with occasional trees or bushes, and (c) wooded. In the west where both species live, *Clausilia dubia* lives in wooded sites while *A. secale* occupies open sites. In the east, however, *C. dubia* becomes abundant in open sites where *A. secale* is absent. Neither microclimatic differences at the sites, nor inter-specific competition seems to explain this distribution.

Abida secale (Draparnaud) has a disjunct, and probably relict distribution in Britain, being found on some, but not all, of the chalk and limestone hills of southern England, and again on the limestone of the northern Pennines (Kerney 1962, Long 1970). One cause of this distribution is the restriction of *A. secale* to open, rocky and calcareous habitats, but this cannot be the whole explanation, as many areas with such habitats (western Ireland, N.W. Scotland, the Peak District, N.E. Wales, the Lincolnshire and Yorkshire Wolds, and some of the southern English downs) lack recent records of the species. Even in N.W. England, *A. secale* is by no means present in all apparently suitable sites, as can be seen by comparing its distribution with that of another rock-loving species, *Clausilia dubia* Draparnaud. *A. secale* is more or less restricted to the west of the Pennine watershed, although there are a few old and unconfirmed records further east. *C. dubia* extends much further east.

In August 1974, we investigated a number of sites potentially suitable for *A. secale*. At some of these sites (marked with numbers in Fig. 1) a thorough search was made, and the snail fauna recorded. Other sites (also indicated by area in Fig. 1) were searched only for *A. secale* and *C. dubia*, and notes were made of their presence and relative abundance. The area concerned is shown in Fig. 1. The sites examined fall into three categories—completely open with no trees or bushes, open but with occasional trees or bushes, and wooded. All sites were on Carboniferous limestone, and all had large quantities of rock exposed as crags, screes or pavements. All sites had either *A. secale* or *C. dubia* or both. A distinction between the habitats of the two species is clearly illustrated in Table 1. *A. secale* occupies more open habitats than *C. dubia*. In the woodland site containing *A. secale*, it was confined to crags at the edge of the wood, whereas *C. dubia* was found throughout. Kerney and Fogan (1969) also report *A. secale* from Oxenber and Feizor Woods near Austwick, but it is clear from their account that it is favoured in the most open parts of the woods.

The change from an area containing *A. secale* to one containing *C. dubia* is often very sharp, and appears to be governed by the shade cast by trees. Inside a small, walled wood at Stennerskeugh Clouds (NY 744008), only *C. dubia* was found. The wall along



Fig. 1. A map showing the positions of sites in this study. ■ = Sites of samples containing *A. secale*. □ = sites of samples lacking *A. secale*. Areas quickly surveyed in which *A. secale* was present shown stippled. Areas without *A. secale* shown by plain broken circles. The Ordnance Survey 10 Km. grid is shown in the margins.

TABLE 1

The numbers of sites containing *A. secale*, *C. dubia* or both, divided by habitat. *These five sites lie to the east of the remainder, see text.

Habitats	Species		
	<i>A. secale</i> only	<i>A. secale</i> and <i>C. dubia</i>	<i>C. dubia</i> only
Completely open	22	5	5*
Open with some trees	0	9	6
Wooded	0	1	3

its eastern edge held both species, *C. dubia* being much the commoner. Craggs outside the wood, separated from the wall only by a path, and partly shaded by the trees from the afternoon sun, also had both species, but with *A. secale* predominating. The limestone pavements and rubble above the craggs held only *A. secale*. Similar situations can be found at Scar Close (SD 7477), where there is a mosaic of bare and scrub covered pavements. Colt Park Wood nearby (SD 7777), where the tree cover is more complete, and where the absence of grazing has allowed the rocks to become covered with vegetation, lacks *A. secale*. Many of the open sites with occasional trees in Table 1 were surrounded by larger bare areas. *C. dubia* was found only near the trees. The extreme isolation of some of the trees suggests that *C. dubia* must live in the bare areas as well, but evidently at much lower densities. In all open sites where *C. dubia* was found with *A. secale*, it was much the rarer, and tended to occur in those sites with the deepest and most extensive grykes.

These results emphasize, rather than explain, the oddity of the distribution of *A. secale* in N.W. England. From them alone, one might conclude that *C. dubia* was a woodland species, tolerant of broken cover, but not of complete treelessness. Consideration of other parts of N.W. England, just to the east, shows that this is not so. The five open sites of this study containing *C. dubia* and no *A. secale* are the most easterly examined; four of them are very close to the Malham area, in which *C. dubia* abounds in open habitats and from which *A. secale* is absent (Cameron and Redfern 1972). Factors other than the presence of trees obviously affect the distribution of these species.

TABLE 2

Number of occurrences of certain species of snail in 10 sites containing *A. secale*, and in 18 sites lacking it, but containing *C. dubia*. All are open, treeless sites.

	Sites with <i>A. secale</i> (maximum 10)	Sites without <i>A. secale</i> (maximum 18)
<i>Carychium tridentatum</i> Müller	2	7
<i>Cochlicopa lubrica</i> (Müller)	3	11
<i>Cochlicopa lubricella</i> Porro	8	16
<i>Pyramidula rupestris</i> (Draparnaud)	10	18
<i>Lauria cylindracea</i> (da Costa)	10	18
<i>Ena obscura</i> (Müller)	0	11
<i>Discus rotundatus</i> (Müller)	9	18
<i>Vitrea crystallina</i> (Müller)	4	12
<i>Vitrea contracta</i> (Westerlund)	10	13
<i>Oxychilus cellarius</i> (Müller)	7	12
<i>Aegopinella nitidula</i> (Draparnaud)	0	14
<i>Clausilia bidentata</i> (Ström)	2	13
<i>Cepaea hortensis</i> (Müller)	0	6
<i>Cepaea nemoralis</i> (L.)	6	10
<i>Trichia striolata</i> (C. Pfeiffer)	1	8
<i>Trichia hispida</i> (L.)	6	10

More information on this problem can be obtained by comparing the snail faunas of 10 open sites containing *A. secale* (including 3 with rare *C. dubia* as well) with 3 open sites from this study, and 15 from the Malham area (Cameron and Redfern 1972) which contain *C. dubia* but no *A. secale*. Table 2 shows the occurrence of the commoner species in the two sets of sites, and indicates that there are differences, presumably microclimatic, between them. The species equally frequent in both sets are rupestral (*P. rupestris*, *L. cylindracea*), cavernicolous (*O. cellarius*, *V. contracta*, *D. rotundatus*) and thus appropriate to rock-rubble habitats (Evans and Jones 1973), or typical of a wide range of calcareous habitats (*C. nemoralis*, *C. lubricella*, *T. hispida*). All the remaining species, more frequent in the *C. dubia* sites, are typical of woodland, or of damper and cooler habitats than others in the table which are equally distributed between the sets. *A. secale* would seem to prefer slightly drier sites than *C. dubia*, a conclusion consonant with the restriction of *C. dubia* to partly tree-covered sites in areas where *A. secale* predominates.

The causes of such microclimatic differences are not clear. Information on rainfall throughout the area (Meteorological Office 1973) does not indicate consistent differences between areas where *A. secale* occurs and those where it does not. The wettest sites are probably at Scar Close (c. 2000 mm or 80 inches p.a.) where *A. secale* occurs, and the range in both areas is from 1000–2000 mm p.a. with an average of c. 1400 mm in both. The absence or rarity of most of the downland xerophiles at these sites emphasizes their general dampness (Boycott 1934, Cameron and Redfern 1972), especially by comparison with Long's (1970) sites for *A. secale* in the Cotswolds.

A temperature-based explanation is likewise difficult (Kerney 1962). *C. dubia* can certainly be found at higher altitudes than *A. secale* in the Pennines (over 2000' on Ingleborough, Stratton 1955), but both in the Jura (Kerney 1962) and the central Pyrenees (Cameron, unpublished) *A. secale* reaches higher altitudes. *A. secale* in the Pennines usually occurs between 900' and 1500' (A. Norris, *in litt.*) but this may reflect the abundance of suitable habitats at these altitudes. There are many records, old and new, at lower altitudes nearer the sea at Morecambe Bay, where there are many low limestone hills.

Unlike the situation in S. England, *A. secale* is often very abundant in this area, often being outnumbered only by *P. rupestris*. It appears to reach its highest densities in bare areas of shattered limestone rubble, and it is rarer on isolated crags and on well preserved pavements with large clints and deep grykes. It is in the latter sites particularly that *C. dubia* may be found alongside *A. secale*.

It is tempting, when faced with complementary distributions of the sort seen here, to conclude that the distributions are in part the consequence of competition between the species concerned. This cannot be proved from distribution data alone (Cain, Cameron and Parkin 1969), and the fact that a close relative of *C. dubia*, *C. bidentata*, is usually associated with it (Stratton 1955) and not with *A. secale*, seems to make it less likely. The determining factors of the distribution of *A. secale* in N.W. England remain a matter for speculation.

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REVIEW

American Seashells The Marine Mollusca of the Atlantic and Pacific Coasts of North America. Second Edition. By R. Tucker Abbott, Ph.D., du Pont Chair of Malacology, Delaware Museum of Natural History. pp. 663, 24 col. plates, numerous text-figures. 1974. (Van Nostrand Reinhold Co. New York). Price £20.

Despite the title of *American Seashells* this second edition is not just an updated version of its predecessor of the nineteen-fifties. This new work is aimed at the professional malacologist as well as the serious amateur, and to this end there is a greatly increased coverage of species described and figured. To quote the publisher's blurb 'all 6,500 known species of marine mollusks living in waters adjacent to North America are listed'. Thus the user of the book is spared the maddening discovery that only selected species have been listed, much less described or figured. A basic list of literature is given which enables the original description to be traced in nearly every case.

More than 2,000 species are described fully, including many of our British species. The descriptions are good and in very many cases further data re life-history and habits are given, with references to the relevant papers. Many synonyms are also given—and indexed.

Despite its title the book includes the pteropods, the sacoglossans and nudibranchs. Among the *Aplysias* it is quite alarming to read of species attaining twelve and fifteen inches in length. Two of the colour plates illustrate nudibranchs; all the New England species illustrated are also British species. (? illusts. ex Alder and Hancock). Text-figures of the shells are mostly excellent but some of the nudibranch figures are inadequate. The twenty-four colour plates are pleasing, although Plate 9 appears to the reviewer to be too pink.

The section of the work headed 'Systematics of the Mollusca' is well done and should be most useful to those aspiring to more than 'collector' status. It seems, however, hardly necessary to instruct readers how to pronounce some scientific names. Such pronunciations often vary according to individual idiosyncrasies. The irritating practice of giving 'popular' names to all the species has resulted in names sometimes of almost pre-Linnean length burdening every page. Prof. Abbott makes a strong plea for the formation of a standard list of common names for seashells, but this (if ever carried out) would merely mean that once the 'sheller' wished to communicate or exchange with overseas correspondents he would have to learn the 'difficult' names anyhow!

The book is well indexed and though large (663 pp.) it is not unwieldy to handle. It is certain to be widely welcomed and much used.

N. F. McMILLAN

THE COMMERCIAL EXPLOITATION OF THE FRESHWATER PEARL MUSSEL, *MARGARITIFERA* *MARGARITIFERA* L. (BIVALVIA: MARGARITIFERIDAE) IN GREAT BRITAIN

THE EARL OF CRANBROOK

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(Read before the Society, 24 April 1976)

Abstract: *M. margaritifera* lives in swift, generally acid, rivers in sand or gravel at a depth of $\frac{1}{2}$ – $1\frac{1}{2}$ m. Post-glochidial mussels burrow in the sediment and the smallest may also be secured by byssus. *M. margaritifera* has been subject to commercial pearl fishing at least since Roman times, but very few full-time professional pearl fishers remain in Britain. They take only mussels over 80 mm long and seldom over-exploit mussel beds. However, some beds have been stripped of juveniles as well and this practice may have contributed to the apparent decline of the species in Britain. Some form of protection may become necessary if the practice continues.

M. margaritifera is a holarctic species found from Iceland through northern Europe and Asia to Japan, and in Canada and the United States. In general it is only found in acid, lime-free rivers flowing from ancient rocks but Boycott (1927) recorded its discovery in the River Nore which flows through limestone in Ireland. It is a long-lived species and it has been calculated that individuals can live to upwards of 90 or 100 years of age. Some produce pearls of varying quality and in many parts of its range it is subject to commercial exploitation. It has been reported as having become rare over much of Western Europe, while in Great Britain from having been recorded from 114 10 Km squares before 1950, it has only been recorded from 37 since that date (M. P. Kerney, unpublished).

Both before and after 1950 all these records are of sites where *M. margaritifera* had been found by the relatively small number of naturalists looking for it and cannot be looked upon as giving an accurate picture of its pre- and post-1950 distribution in Gt. Britain, but these and similar records from other Western European countries are the only evidence available about recent changes in its status. All seem to suggest a decrease in numbers and distribution which has variously been attributed to pollution or over-exploitation by pearl fishers.

HABITAT

Little work has been done in this country on the micro-distribution of *margaritifera* in those rivers in which it occurs but Jackson (1925) reports it as being found where there is a sandy bottom in from $1\frac{1}{2}$ to 4 or 5 feet ($\frac{1}{2}$ – $1\frac{1}{2}$ m approximately) of water. It is not found in deep water and muddy places but on a sandy bottom in shallow water with not too strong a current and in rapids on the sheltered sides of large stones in the sandy gravel which accumulates there. More recently Hendelberg (1960) and Stober (1972), investigating in greater detail the distribution of *M. margaritifera* over about 15 Km of river in Sweden and in a mussel bed 26 m \times 130 m in the United States respectively,

confirm the findings of Jackson: relatively shallow water, running fast enough to prevent the accumulation of silt or mud, in sand or gravel and in patches of smaller material amongst larger stones. Stober only found mussels at depths between 0.5 and 0.8 m, and although Hendelberg found 90% between 0.5 and 1.5 m and none deeper than 2 m, he reports commercial pearl fishing as taking place down to a depth of 5 m.

BREEDING

As in other species of the Unionacea the early stages are spent encysted on fish for a longer or shorter period, depending upon the temperature of the water. When the cyst ruptures the minute mussel falls to the bottom of the river and has to develop or die on the substrate on which it falls. Little is known of the post-glochidial stage in this country since very few juveniles seem to have been recovered. Jackson (1925) had only seen four, the smallest 9.5 and the largest 19 mm in length, and there are in the British Museum (Natural History) 14 specimens from Co. Wicklow in Ireland between 15 mm and 35 mm in length but, as with those reported by Jackson, nothing is recorded about the circumstances of their collection. The four youngest mussels found by Stober (1972) collecting 'with a small rake . . . or by hand picking while diving' were between 69 and 88 mm. However in Japan Koba (1933) found *margaritifera* abundant in 'sand and gravel' and 'sand and coarse sand' at a depth of about 1 m, the larger specimens in sand and gravel with the posterior half or so of their shells sticking out above the substrate, as is commonly observed in this country. In the sand and coarse sand he found a number of smaller specimens and the shells of those between 10 and 30 mm in length were completely buried in the sand and could not be seen. At the most only the black margins of the siphons could be seen as a short black line.

Professional pearl fishers in this country maintain that replacements 'grow up from below' when a bed is stripped of the larger specimens likely to contain a pearl, even though none is obvious to the eye as the experience of Stober (1972) shows. This has been confirmed by Mr. W. Abernethy, a professional pearl fisher like his father before him, who has been good enough to sieve the material below a stripped mussel bed in the River Tay for me, recovering 17 juveniles, four of 11, 11, 21, 25 mm, 6 between 30 and 40 mm and 7 between 45 and 58 mm in length. It seems probable therefore that when a young *margaritifera* falls to the bottom amongst sand and gravel fine enough to allow it to bury itself to the siphons, it can remain protected against such predators as trout and against injury from rolling stones in a spate, during the time when it is still young and relatively fragile. I have known juveniles of *Dreissena polymorpha* to be found in the stomach of trout but while these of course are exposed to view they are protected to a considerable extent by being attached to the substrate by the byssus.

It seems possible that very small juvenile *M. margaritifera* may have the additional security of physical attachment to the substrate in which Koba (1933) has shown that they bury themselves. Isely (1911) found very small juveniles of some American species of Unionacea, though not including *M. margaritifera*, attached by a thread to stones in a coarse gravel bed with pebbles from $\frac{1}{4}$ –1 inch (6–25 mm) in diameter. This thread was strong enough to bear the weight of several small pebbles and he says that the easiest way of finding these very small specimens was to take up handfuls of gravel and look for the threads. Mr. Abernethy found a specimen 11 mm long attached to a small pebble by a thread strong enough to support mussel or pebble hanging free.

PEARL FISHING IN BRITAIN

There seems to have been a pearl fishery in Britain from a very early time. Both

Pliny, in about A.D.70 in his *Natural History* Book II Chapter 57, and Suetonius, in about A.D.120 in his *Lives of the Caesars* XLVII, refer to Julius Caesar's interest in pearls from Britain, while Tacitus, in about A.D.99 in his *Life of Agricola* Ch.13, says that in Britain pearls are found in the sea but are of poor quality, brownish or lead coloured, and compares them unfavourably with those found in the Red Sea. All in all, though the Romans knew that pearls did come from Britain, those oft quoted authors do not seem to have known how or where they were found, though in fact they must have come from *M. margaritifera*. The population in the mountainous districts where *M. margaritifera* is found must have been very small and the effect of pearl fishing negligible. Though a trade in pearls from the whole of the British Isles is well attested from the 12th Century onwards, the human population remained small and the effect of human predation must have remained negligible until the end of the 18th Century.

During the past 200 years or so there seem to have been occasional periods when the demand for pearls became strong and over-fishing resulted. The best documented was in the 1860's when a German merchant called Moritz Unger came to Scotland to buy pearls. He so stimulated pearl fishing that many rivers were fished out and the trade fell away.

As pressure decreased the mussel population increased and by the beginning of this century there was a fair number of people engaged in pearl fishing, mainly in Scotland but to a lesser extent in England and Wales. Since then the number of whole-time pearl fishers has fallen and it seems that now they could be counted on the fingers of one or at most two hands. There is also a fair number of part-timers, the number of whom increases considerably when e.g. the recovery of an unusually large and valuable pearl is reported in the papers. The part-timers in general fish near their homes, but there are still a few travelling tinkers who fish occasionally and of recent years holiday makers and skin divers have increasingly turned their attention to pearl mussels. The whole-timers travel widely to any river in Great Britain in which they know that *M. margaritifera* is found, some apparently going to Ireland or even to Scandinavia.

TECHNIQUES

Until recently mussels were only taken by wading in water not deeper than that which could be fished in breast high waders. Divers in wet suits can fish rivers at any depth, can take mussels by hand instead of looking through a plastic bucket with a glass bottom and using a cleft stick to retrieve the mussels, as those using waders do. When he has collected as many as he can find or, if there are many, as he can conveniently carry, the pearl fisher takes them to the bank, opens them one by one and runs a finger between shell and mantle to feel for a pearl. Whether it has a pearl or not the animal in its shell is thrown back into the water or left on the bank: in either case it dies. It is a destructive fishery but not more so than taking fish or shell fish to sell for food.

EFFECT ON MUSSEL POPULATION

Just as with any other wild species subject to human predation, over-exploitation can be disastrous, as the history of that by Unger in the 1860's referred to above, shows. The tradition of 'German Charlie' and of the results of over-fishing still persists in Scotland. In the case of relatively easily found diurnal creatures, like the Quagga or Passenger Pigeon, the complete extermination of a once abundant species by uncontrolled exploitation is possible. With more secretive nocturnal ones, like the Wild Cat in this country, and others which demand a fairly intensive effort to find them, like *M. margaritifera*, the time comes when it becomes too difficult or hopelessly uneconomic to find and destroy the last

few. Unless the habitat is destroyed by pollution or otherwise, the population gradually builds up again, as happened with *M. margaritifera* in the post-Unger period, and is happening in the case of the Wild Cat in this country today.

Though the species may survive in such cases, the trade on which some people depend for their livelihood will not. In the case of most commercially exploited species either the Government or private owners usually take steps to ensure, by close seasons, protection of juveniles, restriction on numbers taken, etc., that the breeding population is maintained at the level likely to produce the maximum sustainable annual yield.

In the case of *M. margaritifera*, so far as the more knowledgeable whole-time commercial pearl fishers are concerned, juveniles are already protected. Experience shows that mussels under about 80 mm in length are unlikely to produce pearls of any value and if taken they are thrown back unopened as not being worth wasting time on. Moreover, as explained above, the very small ones are not interfered with at all. Such men keep their knowledge of the whereabouts of commercially exploitable mussel beds to themselves, visiting and stripping them of possible pearl bearing shells at intervals of 15 years or so. During that period a mussel 80 mm long will probably have grown by 12 or 15 mm and a small pearl to one of commercial size. Meanwhile the mussels can be producing young ones, and small ones are 'growing up from below'.

There are, however, indications that some pearl fishers whether from ignorance or otherwise, will take, open and kill mussels much less than 80 mm in length. Many leave piles of shells on the bank and the evidence that those smaller mussels are taken is all too obvious. Some local people suggest that these piles are left by holiday makers and in particular by skin divers, whose activities are resented. Salmon and trout fishermen also resent a pearl fisher wading about in the water at the head or tail of a pool which they are about to fish, but in general the few commercial ones are accepted as one of the traditional facts of life. It seems probable that both whole-time pearl fishers and fishermen with rod and line would welcome a system of licensing.

Most of the pearls found by professional pearl fishers seem to be marketed through a single firm of jewellers, Messrs. Cairncross in Perth, who tell me that they deal with less than half a dozen individuals who make their living or a large part of it by pearl fishing. It is an arduous life which involves travelling all over Great Britain and working waist deep in cold water, bent double to search the bottom of the river through a water telescope. Pearl fishing of course is only possible when a river is not in spate and, since lime-free rivers in general only rise in hilly districts with a high rainfall, many days can be wasted waiting for a swollen river to fall. In a day's work several hundreds of mussels can be taken and the fact that even half a dozen people have in the past, and still can, earn a living by pearl fishing, suggests that in this country at the existing level of predation not more than the natural increase is being taken, and that the creature is much more widespread than the reports of field naturalists imply. This is to be expected. A sub-aqua club spent a week-end searching about 2 Km of the River Vernwy above the site where a single dead specimen of *margaritifera* had been found and only found 2 solitary live individuals, each one in sand behind a large rock in rapids (A. Stevens, unpublished). Hendelberg (1960), after a careful search, found mussel beds in four relatively limited regions in a stretch of 15 Km. Professional pearl fishers would probably know of the beds but would not advertize them: few naturalists making a general survey could spare the time to search as diligently.

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FIELD OBSERVATIONS ON *THEBA PISANA* (MÜLLER) (GASTROPODA: HELICIDAE) AT ST IVES, CORNWALL

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(Read before the Society, 15 May 1976)

Abstract: Two colonies of *Theba pisana* (Müller), of 6-700 and 75-100 individuals, are established at St. Ives, Cornwall, where formerly more extensive areas were colonized by the species. *T. pisana* is the dominant snail within the colonies which occur on the lower slopes of 'The Island' where soil pH is 6-7.5. Food plants include varieties of plantain (*Plantago*), sea carrot (*Daucus carota gummifer*) and, in the smaller colony, sea beet (*Beta vulgaris maritima*). Factors determining activity within the colonies include wind force and direction, but rainfall and the amount of moisture on vegetation were dominant. *T. pisana* is a nocturnal species, with daytime activity strictly controlled by the prevailing weather conditions. The area in which an individual snail moves within a colony is small, which correlates with the poor ability of the species to disperse by natural means. The spread of the colonies is also restricted by building developments. *T. pisana* at St. Ives is not apparently subject to mammalian or avian predation, nor to parasitic infestation. It was found buried in the soil in December, February and March, down to 3 cm below surface. Factors causing burial remain uncertain. Polymorphism of *T. pisana* is limited here; only four varieties and sub-varieties have been recorded.

St. Ives Head, or the Island, (National Grid reference 10/521410) is the only known site in England where a colony of the sandhill snail, *Theba pisana* (Müller), survives. The species was first recorded at St. Ives in 1797 by W. G. Maton. In 1841 the Cornish naturalist Jonathan Couch also noted that *T. pisana* was to be found in the district 'where it exists in profusion'. Several conchologists writing in the 19th century acknowledged the presence of the snail at this station, most of whom indicated that it was far more prevalent around the locality than is the case today.

Intensive searches have failed to reveal any further colonies of the snail at St. Ives. A number of localities displaying environmental characteristics which superficially appear to be favourable for the species to thrive in, have so far proved to be disappointing. Nor during the two years in which the colonies were under observation for the purpose of this study (1974-75) was any significant extension of those areas already occupied on the Island recorded.

The present colonies of *T. pisana* are restricted to two small and isolated areas on the Island, the smaller colony not having been previously reported (Turk 1966). Factors limiting the growth of these two colonies, and the activities of individual snails are discussed in the light of daily observations made over a period of twelve months.

THE SITES AND SIZES OF THE POPULATIONS

Although now a geographically integrated part of the mainland, it has been shown that in recent historic times the Island was an isolated piece of land, surrounded by the sea (Noall 1958). According to Noall 'it may reasonably be inferred that the old channel which divided St. Ives into two distinct parts, ceased to exist, as such, between the years 1642 and 1645'. Today the Island is joined to the mainland by a raised beach and 'head' which has been extensively built over. There is no evidence, documentary or archaeol-

ogical, to suggest that *T. pisana* was introduced to this Cornish locality before the marine channel ceased to exist. It is therefore unlikely that this topographical aspect has played any significant part in determining the present distribution of the species at St. Ives.

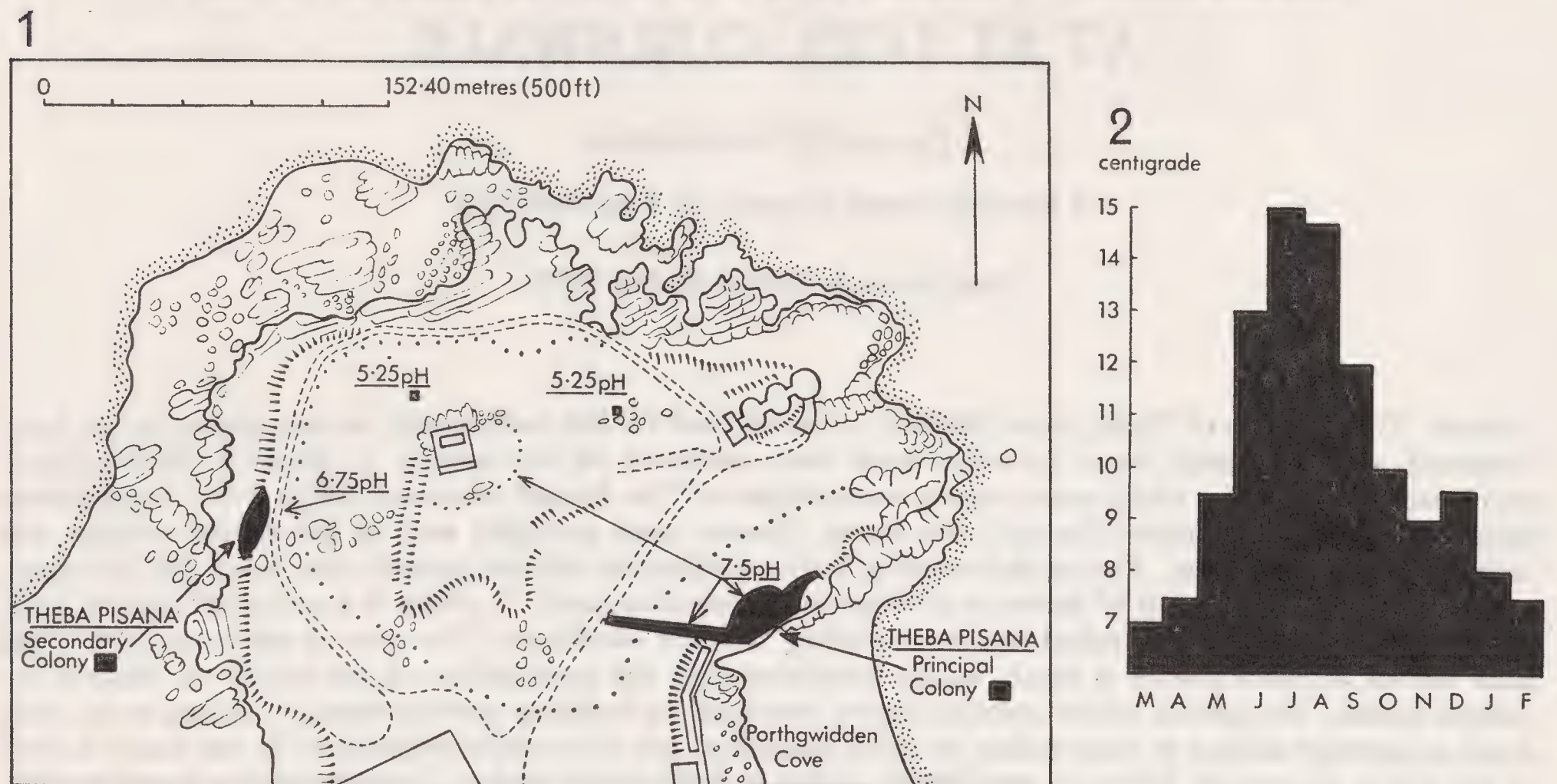


Fig. 1. St. Ives Head or The Island, showing the distribution of *T. pisana* and pH readings.

Fig. 2. Histogram showing mean monthly temperatures (°C) recorded at 23.00 hours on the Island, March 1974 to February 1975.

The principal colony (Fig. 1) maintains a stable population of between 600 and 700 individuals at all stages of growth, in an area of approximately 216 m². This site is concentrated on a near vertical bank composed of 'head', which is unstable and subject to small falls during severe weather conditions, and which forms part of the cliff face on the south-east flank of the Island. It is 54 m in length, varying in height from between 3 and 5.5 m, and with a minimum height of 9 m above the normal beach level. The colony is exposed to south and east winds which blow across the site unchecked. Since it is situated at the edge of the splash-zone, sand and sea-spray are regularly deposited along the entire length of the bank notably during storms, and assist in maintaining the essential highly calcareous soil. Some protection from the north and west winds is afforded by the steep ascent of the Island to the rear, rising to a height of 33.20 m above sea-level.

A small proportion of the snails belonging to this colony, perhaps 2% to 3%, thrive on the level ground above the bank. Some are associated with a small patch of winter heliotrope (*Petasites fragrans* (Vill.) C. Presl.) which flourishes in the lee of a low mound, while others inhabit a line of rocks placed along the boundary of the adjacent car park. A network of footpaths, which are used extensively throughout the summer months, together with the predominantly short turf which is occasionally mown for recreational purposes, rigorously control the small numbers which do manage to survive in this area. This aspect is generally true of the Island as a whole, and is probably the main influence restricting the expansion of the colonies beyond their present boundaries.

The second colony, which faces the Atlantic on the west side of the Island, is equally exposed. Here the full force of the north and west winds blows directly onto the site. Approximately 75 to 100 specimens occupy this area, which, like the previous colony, is established on the side of a steep bank, rising 13 m above the normal beach level. In

all, the area is no more than 7 m in length. Once again the presence of public footpaths, including one of tar-macadam immediately above the colony, severely contains the snails within the existing boundaries.

GEOLOGY

The Island is composed of one of three coastal outcrops of intrusive greenstone found along the west coast of Penwith and associated with the granite mass. At St. Ives this greenstone is variable in texture, but commonly a very fine holocrystalline type, almost black in colour. In addition a grey-green un laminated slate, which is considerably eroded along the northern shoreline of the Island, is also exposed. On the south side of the Island, in Porthgwidden Cove, occurred the only local example of a raised beach, now obliterated beneath a concrete esplanade and above which the principal colony of *T. pisana* is established. The Island is encircled by large exposures of loose 'head' or drift rubble, which has accumulated above the greenstone to a depth of 4 m, and consists of brown clay, sand and local rocks.

FOOD SOURCES AND SOIL

Although the flora on the Island is deficient in many of the food plants listed elsewhere, it is obvious that the dietary range of *T. pisana* is extremely variable, and is controlled by the type of plants locally available. The significant food plants at St. Ives, and on which *T. pisana* has been observed feeding, are species of plantain, particularly sea plantain (*Plantago maritima* L.), sea carrot (*Daucus carota* subsp. *gummifer*) and smooth sowthistle (*Sonchus oleraceus* L.). A few stragglers belonging to the principal colony do exist within a large patch of winter heliotrope (*Petasites fragrans* (Vill.) C. Presl.). They have not been seen to feed on these plants and it is therefore doubtful whether the heliotrope has the effect of enticing the snails away from the main population where it is absent. Sea plantain is not found on the west-facing site, where the vegetation offers less variety. Here sea beet (*Beta vulgaris* L. ssp. *maritima* (L.) Thell.), which is absent in the south-east area, may be added as an important substitute to the food source list. These food plants are by no means confined to those areas occupied by *T. pisana*, a factor which discounts any suggestion that the distribution of the food supply is responsible for the location of the present colonies. In addition it may be noted that the carnivorous habits of *T. pisana* have already been remarked upon (Step 1945 and Cooke *et al.* 1895). Both authors relate how *T. pisana* devoured specimens of *Helicella itala* when the two species were confined together. *H. itala* has not been recorded on the Island and such carnivorous habits have not been observed towards any of the other species present.

The vegetation on the south-east site, although generally dense, particularly so at the top of the bank, is nevertheless uniformly low, rarely exceeding 30 cm in height. Direct exposure to the south and east winds is undoubtedly responsible for this restriction on growth. The level ground above the bank is well-trodden during the summer months by many thousands of tourists, who effectively crop the vegetation, and who also act as a deterrent to the expansion of the colony in this direction.

The structure of the soil on the south-east bank is basically a light sandy mixture, although areas of medium to heavy loam are present on the slopes above. It should be noted that there are no sand dunes or areas of pure sand on the Island. However, considerable quantities of wind-blown sand are deposited along the entire length of the bank from the surrounding beaches. Soil tests on this site reveal its calcareous nature, giving a consistent reading of 7.5 pH at all levels (Fig. 1).

The vegetation on the west-facing site is very sparse and unevenly distributed. Growth on top of the bank is retarded by the presence of a tar-macadam footpath; while below, rocks from the beach extend almost up to the top of the bank, leaving only a narrow strip, less than 2 m wide, where the plants are able to establish themselves. It is a predominantly bare and rocky situation. The soil here is yellow and heavy, with a sticky clay-like texture. The difficulty experienced by the snails in burrowing into this surface, coupled with the meagre plant life, must be responsible for the small size of this colony and exclude the possibility of any further increase in the numbers found here. A series of soil tests showed readings of 6.75 pH overall, a reduction from the higher level noted on the south-east site (Fig. 1).

LIST OF FLORA

At least 130 species of ferns and flowering plants have been recorded on the Island (Turk 1972b and Renwick 1974). 64 of these have been noted within the areas occupied by *T. pisana*, and to assist matching the flora of this original site with possible future sites for the reintroduction of the species, these plants have been listed below.

- | | |
|--|---|
| <i>Anthyllis vulneraria</i> L. | <i>Armeria maritima</i> (Mill). |
| <i>Crithmum maritimum</i> L. | <i>Potentilla reptans</i> L. |
| <i>Potentilla anserina</i> L. | <i>Ranunculus repens</i> L. |
| <i>Ranunculus ficaria</i> L. | <i>Salvia horminoides</i> (Pourr). |
| <i>Rumex pulcher</i> L. | <i>Rumex obtusifolius</i> L. |
| <i>Rumex crispus</i> L. | <i>Bellis perennis</i> L. |
| <i>Medicago arabica</i> (L) Huds. | <i>Medicago lupulina</i> L. |
| <i>Veronica chamaedrys</i> L. | <i>Cochlearia danica</i> L. |
| <i>Cirsium vulgare</i> (Savi) Ten. | <i>Sonchus asper</i> (L) Hill. |
| <i>Sonchus oleraceus</i> L. | <i>Plantago lanceolata</i> L. |
| <i>Plantago maritima</i> L. | <i>Plantago coronopus</i> L. |
| <i>Senecio vulgaris</i> L. | <i>Senecio jacobaea</i> L. |
| <i>Daucus carota</i> L. ssp. <i>gummifer</i> . | <i>Festuca ovina</i> L. |
| <i>Dactylis glomerata</i> L. | <i>Festuca rubra</i> L. |
| <i>Spergularia rupicola</i> Lebel ex Le Jolis. | <i>Agrostis stolonifera</i> L. |
| <i>Petasites fragrans</i> (Vill) C. Presl. | <i>Tripleurospermum maritimum</i> L. Kock. |
| <i>Diploxaxis muralis</i> (L) D.C. | <i>Beta vulgaris</i> L. ssp. <i>maritima</i> (L) Thell. |
| <i>Ononis repens</i> ssp. <i>repens</i> L. | <i>Cerastium holosteoides</i> Fr. |
| <i>Achillea millefolium</i> L. | <i>Cirsium arvense</i> (L) Scop. |
| <i>Lotus corniculatus</i> L. | <i>Heracleum sphondylium</i> L. |
| <i>Anagallis arvensis</i> L. | <i>Taraxacum officinale</i> Weber s.l. |
| <i>Geranium molle</i> L. | <i>Centaurea nigra</i> L. |
| <i>Ballota nigra</i> L. ssp. <i>foetida</i> Hayek. | <i>Convolvulus arvensis</i> L. |
| <i>Lolium perenne</i> L. ssp. <i>perenne</i> . | <i>Poa annua</i> L. |
| <i>Trifolium occidentale</i> D.E. Coombe. | <i>Poa pratensis</i> L. |
| <i>Trifolium scabrum</i> L. | <i>Catapodium maritimum</i> (L) C.E. Hubbard. |
| <i>Atriplex patula</i> L. | <i>Trifolium repens</i> L. |
| <i>Bromus mollis</i> agg. | <i>Trifolium dubium</i> Sibth. |
| <i>Hypochaeris radicata</i> L. | <i>Galium aparine</i> L. |
| <i>Leontodon taraxacoides</i> (Vill) Merat. | <i>Parietaria diffusa</i> Mert. and Kock. |
| | <i>Malva sylvestris</i> L. |
| | <i>Crepis capillaris</i> (L) Wallr. |
| | <i>Leontodon autumnalis</i> L. |
| | <i>Agropyron repens</i> (L) Beauv. |

MOLLUSCS RECORDED ON THE ISLAND

An additional 19 species of terrestrial molluscs have been recorded on the Island and more than half of these have been found in varying numbers among the colonies of *T. pisana*.

Cochlicopa lubrica (Müller). Locally common; occasional on the south-east bank.

Lauria cylindracea (da Costa). Locally common; frequent on the south-east bank. This species is often found hibernating inside dead shells of *T. pisana* during the winter months.

Testacella maugei Férussac. Scarce.

Helix aspersa Müller. Common. With *C. acuta* this is the species most commonly found in association with *T. pisana*. An average of 50 or more adults are normally resident within the area of the principal colony.

Ashfordia granulata (Alder). Common; frequent on the south-east bank.

Candidula intersecta (Poiret) = *Helicella caperata* (Montagu). Locally common. Frequent with *T. pisana* on the south-east bank.

Ceruella virgata (da Costa). Abundant; common among both colonies of *T. pisana*.

Cochlicella acuta (Müller). Common; particularly on the south slope of the Island. Frequent among the principal colony of *T. pisana* where it breeds prolifically.

Arion intermedius Normand. Occasional.

Arion ater rufus (L). Occasional.

Oxychilus draparnaudi (Beck). Common; frequent among the south-east colony of *T. pisana*.

Aegopinella nitidula (Draparnaud). Occasional; occurs with *T. pisana*.

Vitrina pellucida (Müller). Occasional on the south-east bank.

Milax gagates (Draparnaud). Occasional.

Milax sowerbyi (Férussac). Occasional.

Limax maximus L. Common.

Limax flavus L. Occasional.

Deroceras reticulatus (Müller). Common.

Deroceras caruanae (Pollonera). Occasional.

FACTORS DETERMINING ACTIVITY

Temperature. (Fig. 2) Cornwall enjoys a warm and humid climate and is noted for its moderate, though predominantly wet, winter period. Frost is unusual; in the extreme south-west it does not normally occur at all, particularly in those districts adjacent to the coast.

The winter of 1974–75 proved to be typically mild. Temperatures were recorded on the Island for a total of 319 days, from March 1974 to February 1975 inclusive. Readings were taken at ground level from the principal colony at approximately 23.00 hours each day. On this basis it can be seen from Fig. 2 that the lowest mean monthly temperatures occurred in February, March and April, with readings of 7.2°C, 7°C and 7.5°C respectively. However, individual daily readings of 9°C and 10°C were not infrequent and persisted throughout the winter months. In comparison the peak summer temperatures occurred in July (14.8°C) and August (14.5°C). When set against the representative winter months a mean differential of about 7.5°C is evident.

Temperature variations experienced in an average winter at St. Ives are not a critical factor determining periods of activity among *T. pisana*. This seasonal variation is remarkably moderate, due mainly to the maritime situation where the colonies are established. The number of active specimens may at times be very small, as Fig. 3 shows, but a decrease in temperature alone was not at any time considered to be the prime cause for this reduction. In this connection it is significant to note that on the night which gave the lowest temperature reading, 2°C, approximately one dozen *T. pisana* were observed to be active.

Wind. To a considerable extent the direction and force of the wind are crucial factors determining the level of activity of *T. pisana*. The direct exposure of the principal colony

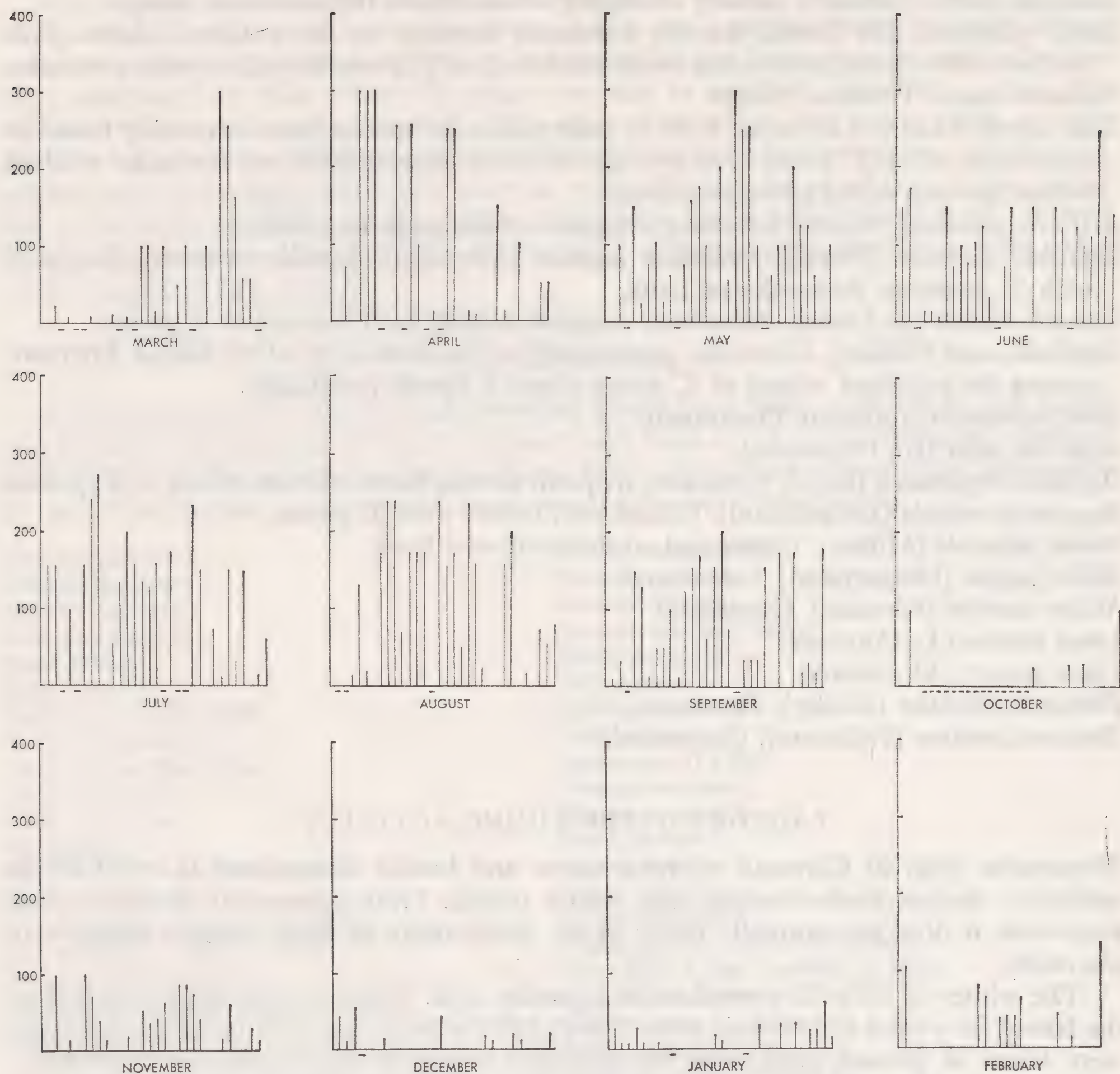


Fig. 3. Histograms showing the number of adult *T. pisana* active at the principal colony each evening between 22.00 and 24.00 hours, from March 1974 to February 1975. A dash below the base line indicates that no observation was made.

to the full force of south and east winds has a marked influence on activity. In particular the cold easterly winds severely restrict movement mainly because they quickly cause the ground to become dry, in addition to the effects of the actual force of the wind blowing across the site. East winds occurred on 55 out of 319 days on which data relating to specific wind force and direction were recorded between March 1974 and February 1975. *T. pisana* was active on 18 of these days, although always in small numbers. On only three occasions when activity did occur was the wind force greater than 4, force 1 or 2 being more usual. Significantly, of the 35 days on which activity did not occur, 23 days recorded wind speeds of force 4 or over.

An almost reversed situation was evident when the wind veered to a south or south-west direction, to which the principal colony is equally exposed. The southerly winds were nearly always associated with wet conditions, frequently a heavy evening dew, or more often, showers or prolonged periods of rain. *T. pisana* was influenced to a consider-

able extent by these wet cycles, which were found to ameliorate the adverse effects of the southerly winds. Consequently a greater amount of activity was recorded throughout these periods. From a total of 55 days during which the wind originated from this direction, *T. pisana* was active on 39 days. The fact that almost half of these days registered wind speeds of force 5 or over, on several occasions force 7 was recorded, emphasizes the tolerance of the species to winds of near gale force blowing directly on to the site, provided that they are tempered by moist conditions and moderate temperatures. In contrast, on the few occasions when spells of easterly winds were accompanied by damp conditions, the direct effects of the wind were clearly paramount, with the result that activity did not usually occur.

The reactions of the principal colony to the wind from either a northerly or westerly point are less evident. As already noted, virtually complete protection is afforded from the north, and only to a slightly lesser extent from the west. Consequently these winds do not motivate or retard activity to any significant degree at St. Ives. Winds from these quarters occurred on 129 days, or 40.4% of all the records collected.

Rainfall. The amount of rainfall recorded at St. Ives for the twelve months under observation is set out in Fig. 4. It was a particularly wet autumn and first winter period, September, November and January each had high levels of rainfall in excess of 170 mm. August was also notably wetter than average. The total rainfall for March 1974 to February 1975 inclusive amounted to 1250.5 mm.

Moist conditions appreciably increase the chances of activity taking place, and it must be considered as a more important factor in this respect than either wind or temperature. Nevertheless, a noticeable reduction in activity occurred when heavy rain was actually falling. Recorded fatalities have resulted from the snails soaking up excessive moisture (Turk 1972a), and the sensitivity of the species to this danger is apparent, with a minimal amount of activity being observed at such times. Conditions appeared to be most favourable when light rain or mist occurred, and large numbers were frequently observed during these periods. Despite the fact that moist conditions facilitate activity, it is likely that the tolerance of the species to a wet habitat approaches its limit on the south-west peninsula of Cornwall, where 1500 mm of rain can fall annually. Some significance may be attached to the fact that the two colonies at St. Ives are both situated on the sides of steep banks, providing adequate drainage. Montagu (1803) also noted that the snail was established 'on the slope of the hill' at St. Ives, a fact which may further emphasize that effective drainage has always been essential for the species to maintain its presence in this locality.

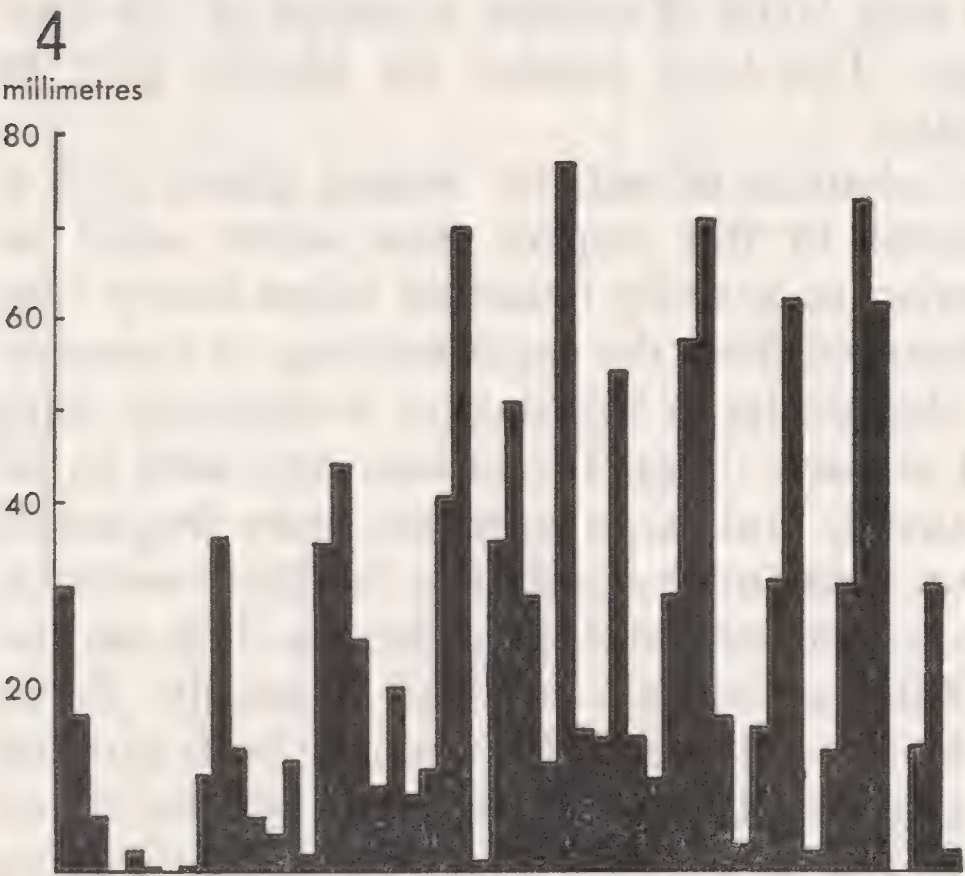
The extent to which moisture on the ground influences activity may be demonstrated by an analysis of the movements in the principal colony made during the predominantly wet month of August. The data have been collated from a total of 28 daily observations. Rain or heavy dew was recorded on 18 days and *T. pisana* was active on each of these, often in considerable numbers (Fig. 3). Of the remaining 10 days on which the ground was dry, activity occurred on only 2 days. Throughout the month both wet and dry periods showed identical fluctuations in wind and temperature, light westerly winds interspersed with calm periods, and a mean temperature of $14.5^{\circ}\text{C} \pm 2.5^{\circ}\text{C}$. The absence of extreme fluctuations by these supplementary factors provided a sufficiently stable condition within the colony on which to assess the effects of moisture, and the month as a whole effectively illustrates the correlation existing between rainfall and activity.

Intermittently throughout the year, numbers of *T. pisana* were observed in an active state when the ground and vegetation were completely dry. However, it was evident that the additional factors regulating movement, wind and temperature, were nearly always favourable. If the dry period persisted for several days, activity usually ceased,

regardless of the influence exerted by the other factors. Although there were occasions when the species engaged in activity during dry spells, indicating that moisture is not entirely essential, nevertheless, the rapid increase in numbers which emerged with the onset of light rain or dew, illustrated the strong preference for some degree of moisture on the ground.

Daylight. Little or no activity was observed during the daytime, and *T. pisana* must be considered as essentially a nocturnal species. Limited activity was occasionally prolonged into the early morning, when individuals still preparing to aestivate or descending into the undergrowth, were observed. The weather considerably influenced the extent of this early morning activity, with wet or overcast conditions markedly reducing the instinct to retire. Even so, activity was not observed to occur generally after 11.00 hours, either during the summer or winter months, except for occasional isolated specimens noted later in the day.

Movement would commence again an hour or two earlier than normal in the evening, if the conducive weather conditions persisted. However, the majority of the population was not activated until darkness finally closed in, and in the absence of rain, a reasonable amount of dew had formed on the vegetation.



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NUMBER	1	2	3	4	5	6	7	8	9	10
MAY	0	0	0	0	0	0	0	0	0	0
JUNE	0	0	0				0	0		
JULY	0	0					0	0		
AUG	0	0					C	0		0
SEPT	0		B							0
OCT	0									
NOV	0									
DEC	A									D

Fig. 4. Histogram showing the weekly rainfall, measured in mm, recorded at St. Ives for the period March 1974 to February 1975.

Fig. 5. Monthly observations relating to ten specimens of *T. pisana* whose shells were marked on 24 April 1974. (O) Indicates that the specimen was located at least once during the month within a one metre radius of the point at which it was released. (A) Found dead and unmoved, 14 December 1974. (B) Found dead and unmoved, 29 September 1974. (C) Last recorded live 12 m from the point of marking. (D) Found dead and unmoved, 30 December 1974.

BURROWING

Although *T. pisana* has been cited (Taylor 1912) as being a species susceptible to burying itself in the sand during periods of excessive heat, very little corroborative observation relating to this habit in the British localities has been undertaken. As a result a careful watch on the St. Ives colonies has been kept in an attempt to establish the prevalence of this activity and it has, in fact, proved to be a feature in the behaviour pattern of the species, although occasional and irregular. No *T. pisana* were ever located buried in the summer months. The abundant herbage covering the south-east site

effectively prevented an intensive search of the ground from being carried out during the summer without inflicting unnecessary damage to the plants. Nevertheless, small random areas were searched, usually during hot and sunny weather conditions, and no specimens were found to have buried themselves. Conversely the more usual habit of the species of aestivating on the vegetation is not so common at St. Ives as it has been reported to be elsewhere (Barrett 1972 and Pitchford 1974 *in litt.*). Most of the snails descend to the shade offered at the base of the plants, especially beneath the more compact species such as *Plantago maritima*, to which they attach themselves in the early morning. *T. pisana* normally remained in this position throughout the day.

More positive results were obtained when searches conducted in the winter months revealed live snails buried in the sandy loam which underlies the south-east site. In late December 1974 several specimens were located buried, with a maximum of 3 cm of fine loam covering the shells. The mouths of these snails were without any trace of a recent epiphragm. Again in February 1975 up to ten individuals were found buried at approximately the same depth. Two of these specimens possessed opaque white, brittle epiphragms constructed at the extreme edge of the mouth. This was the first time that this type of epiphragm had been observed. It had not been seen among those specimens encountered aestivating in the previous summer period, although the typical translucent epiphragm was much in evidence. In fact no opaque epiphragms were ever found on *T. pisana* collected above the ground, and of the subsequent specimens unearthed very few displayed traces of this opaque type. Finally during the following March, after a prolonged spell of easterly winds, several specimens were again recorded buried under the fine humus, in this instance with the mouths of the shells turned downwards, in depths just sufficient to cover the tips of their spires. None of these snails possessed epiphragms and although, as on this occasion, such shallow excavations are consistent with egg laying activity, no deposits of eggs were located.

The relatively stable structure of the top soil covering the principal colony, consolidated as it is by a tight mass of vegetation throughout the year, excludes the possibility that those snails found buried may have been trapped while inert on the surface and were consequently covered over by wind blown sand and debris. It is therefore apparent that *T. pisana* does bury itself, although perhaps only to a limited extent and principally in the winter months. Insufficient observations have not enabled this activity to be correlated with any specific environmental factor. However, with the evidence that is available, it may be tentatively suggested that a sudden drop in temperature or a prolonged period of cold weather, partially, if not wholly, motivates the snails to attempt to retire below the surface.

DISPERSAL AND INTER-SPECIFIC COMPETITION

T. pisana, essentially a Mediterranean species, has found at St. Ives a congenial niche which in the past extended beyond the confines of the town, but is now reduced to two small colonies on the Island. The pressures of development, mainly related to the increased tourism in the area, have rendered the survival of these colonies uncertain. Some method of dispersal would therefore appear to be necessary if the species is to maintain its presence at this locality.

The extent to which dispersal should be assisted by the artificial colonization of suitable areas is at present being considered. In 1965 Professor Charles Thomas removed several specimens of *T. pisana* from the colony at St. Ives and attempted to establish them on the opposite side of St. Ives Bay, at Gwithian Towans (Turk 1966). Successive searches in this area have failed to reveal the existence of the snail, and it must be assumed that the sites selected for the experiment did not meet with the requirements of the

species. It is hoped that these observations will provide a more detailed knowledge of the specialized habitats necessary to assist in the successful introduction of the species to new sites.

Regrettably it is now impossible to determine whether in the past, snails belonging to the colonies on the Island had access to a direct route with those colonies situated on the slopes above the town. Today houses and other buildings encircle the Island. In addition, the absence of gardens over a wide area close to the sites has severed the important network of herbage usually encountered in small towns. As a result the Island has been isolated from the outlying coastal vegetation, effectively removing the natural routes for land-borne dispersal. Further 'improvements' around Porthgwidden Cove, in particular the construction of a terrace of bathing accommodation, have not only destroyed a considerable amount of territory previously occupied by *T. pisana*, but have also encouraged further disturbance of the site by attracting more visitors to the area. As already noted, the footpaths on the Island are a contributory factor impeding expansion.

With the development of the Cove in 1955, the restricted environment in which the snails belonging to the principal colony found themselves became more acute. This does not, however, appear to have resulted in over-crowding on the site. An abundance of vegetation, lack of disease and an apparently uninterrupted breeding cycle, all indicate the relative stability within the colony. To what extent other behavioural habits have been affected is not certain. As noted in the following section, the marked lack of movement among individuals within the colonies may be characteristic of a species which finds itself already confined to a restricted area. In the absence of any large scale predatory activity by birds or mammals, it is possible that the colony has evolved in isolation some means of preventing an expansion of the population beyond the limits which the site is capable of sustaining, though what these means are is not known.

T. pisana is the numerically dominant species in those areas in which it occurs. During the period in which observations were made, no indication of inter-specific competition was evident. Those species which co-exist with *T. pisana* do not appear to exceed the populations normally expected to occur within such an area and the threshold of inter-specific tolerance is not visibly strained. This lack of competition may be further assisted by the apparent zoning of the feeding areas among different species of snails. At least one of those present (*Helix aspersa*) tends to feed at a lower level of the vegetation. Owing to its large size and weight, this snail is unable to maintain a hold on the delicate foliage of certain types of plants, for example sea carrot, an important food source for *T. pisana*. Normally, therefore, *H. aspersa* will be found feeding towards the bottom of the plant, or more often on a species more capable of sustaining its greater weight, in particular the varieties of plantain. *T. pisana*, which is substantially lighter, is suited to exploit this situation, and may be seen hanging precariously on the extremities of the most fragile plants while feeding.

INDIVIDUAL MOVEMENT WITHIN THE PRINCIPAL COLONY

In order to determine the extent of local movement and its effect within the principal colony, several specimens of *T. pisana* were collected and marked in April 1974. The shells were identified with paint and numbered from one to ten. They were then released in pairs at intervals along the south-east bank, each snail being returned to the exact position from which it had originally been collected. This method reduced the chances of any attempts to move by the snails which may have resulted from their displacement into an unfamiliar locality.

At the end of the first month none of the snails had moved outside an area of one metre radius from the point at which they had been set free (Fig. 5). In June 50% of

the snails could be located, all of which continued to inhabit this severely restricted area and no outward movement had taken place. Four months later in August, at a time when searching for the marked snails became extremely difficult due to the advanced growth of the vegetation, 4 snails could still be found, each one continuing to inhabit the same one metre radius area in which it was first released. Following a series of intermittent observations, a final sighting was made in December 1974, when two specimens were found eight months after being marked. These also had remained unmoved in the restricted area in which they were first released. Throughout the duration of the observations only one snail was noted to have moved significantly outside the one metre radius. This specimen was last recorded live at a distance of 12 m beyond the point of release, having been recorded static during the previous three months. Unfortunately this was the last record obtained relating to this specimen. As shown in Fig. 5, three specimens were recorded dead; they also had remained unmoved during the periods in which they were observed alive.

Twelve months later a similar experiment was carried out. This involved releasing a dozen marked specimens of *T. pisana* together in a concentrated area which was situated at the opposite end of the site from where they had been collected. Once again observations tabulated over a period of two months showed a complete absence of outward movement. These snails settled immediately into their new surroundings, which in almost every respect were identical to those from which they had been taken, and no attempts were made to return to the areas of origin.

It is apparent from the evidence gathered to date that the species at St. Ives possesses no compelling instinct to move within the colony. This lack of movement has already been discussed in relation to its effects on dispersal and the expansion of the present colony. The reasons for the absence of any wide-ranging movement, and the apparent acceptance of almost any micro-habitat within the areas already colonized by the species, are not clear. However, in view of the adequate food plants which cover the area and the general uniformity of the habitat with its clearly defined restrictions on expansion, there appears to be little reason why any large scale movement over the area should be necessary.

PREDATORS AND PARASITES

Both colonies of *T. pisana* appear to be virtually free from the ravages of predators and parasites alike. Indeed if either predation by birds and mammals or a major parasitic attack occurred, it is likely in view of the comparatively small numbers of snails present, that the survival of the colonies would be seriously jeopardized.

The Island is apparently totally deficient of mammals (Turk 1972b). This is probably the result of protracted human pressure on a site already lacking extensive ground cover. This absence is further reinforced by the geographical isolation of the site from the outlying countryside. Examples of characteristic gnawed mollusc shells, denoting attacks by mice or other small rodents, are completely absent.

A wide variety of migratory birds visit the Island throughout the year, although no evidence has been obtained to suggest that any of these species include *T. pisana* in their diet. Song thrushes (*Turdus philomelos* Brehm.) are resident, but they do not breed on the Island. However, no predatory activity by this mollusc-feeding species has been noted and no 'thrush-stones' have been located in the immediate vicinity.

In addition *T. pisana* must be considered a potential recipient of infestation by the glow-worm (*Lampyrus noctiluca* L.) which has been recorded within the appropriate 10 Km square SW54 (Murphy 1971). However, observations to date have proved negative among the St. Ives colonies.

Similarly the snail-killing fly, *Salicella fasciata* (Meigen), which has been recorded

active among the colonies of *T. pisana* at Tenby, South Wales, (Knutson *et al.* 1970) has not been noted at St. Ives. A report that adult specimens of this fly have occurred in the sandhills at Padstow, Cornwall, (Lamb 1904) suggests that the species could well occur within the St. Ives locality.

VARIETIES AT ST. IVES

The shell of *T. pisana* is exceptionally polymorphic. (Taylor 1912) listed numerous varieties, although many of those which he records have never been fully described or illustrated. In addition to 2 forms of monstrosities he lists a total of 9 varieties relating to form, size and substance with 34 sub-varieties, and a further 13 varieties with 32 sub-varieties allied to colour and markings.

Fewer sub-varieties are found at St. Ives than are known to occur in Guernsey or at Tenby, South Wales (Pitchford 1973 and *in litt.* 1974). This may be associated to some extent with the restricted area colonized by the species, and also the essentially uniform type of habitat which exists at St. Ives, the two factors combining to reduce both the opportunity and need for variable forms to develop. Two colour sub-varieties have been found to be dominant on the Island, *interrupta* (Moquin-Tandon) and *subzonata* (Bourguignat). The rose-tinted *faux-rosea* (Monterosato) is not uncommon, although the colouring is generally rather pale. This prevalence of pale and broken shell patterns fully agrees with the type expected to occur in an exposed maritime habitat, such as that found at St. Ives.

With one exception, the variety *depressa* (Requien) which is relatively common, very little variation in the size and form of the shell has been noted. Specimens which can be assigned to those varieties recorded as being larger than type are absent. Most adults attain a diameter of 18 mm, the largest single specimen collected measured 20 mm in diameter. There is also no evidence that any monstrosities have occurred in the past on the Island and no such specimens were recorded in 1974-75.

DISCUSSION

The continued presence of *T. pisana* at St. Ives provides clear evidence that the species is capable of tolerating a considerable and protracted amount of human disturbance. The interference at the principal colony experienced over the last twenty years has originated exclusively from the demands made by the tourist industry in the area. Pitchford (1973 and *in litt.* 26.XII.1974) in particular, has recorded similar pressures exerted on the colonies at Guernsey and Tenby resulting from tourism in those areas. This appears to be the common fate of *T. pisana* throughout the British Isles where the species is invariably established at coastal localities, and as a consequence is subjected to the severe environmental pressures currently experienced by many of these maritime habitats.

Before the colonies at St. Ives were rediscovered (Turk 1966), substantial areas of Porthgwithen Cove, which were occupied by *T. pisana*, were levelled and a terrace of bathing chalets built on the site. When the principal colony was rediscovered it was found to survive only on a relatively small and undisturbed bank situated at the extreme corner of the cove. The secondary colony undoubtedly existed at this time, but due to the unlikely aspect of the site and the small numbers of snails settled there, it failed to attract attention and remained undiscovered until 1974. No appreciable decrease of the principal colony has occurred during the last ten years, either in the total area occupied or in the numbers of snails occurring there. Nevertheless, as a direct result of the increased tourist facilities in the area, this colony has now been extended to the limits of the available

habitat. Coupled with the effective curtailment of the natural routes for dispersal the uncertainty with which these colonies maintain themselves is apparent.

The habitats at St. Ives are dissimilar from those found elsewhere in the British Isles in several respects, two of which require special comment. First is the pattern of vegetation which characterizes the Cornish locality. Both sites are deficient in any herbage exceeding 30 cm in height, the general appearance of the ground cover is that of a short dense grass sward. In contrast Barrett (1975), referring to the colonies in Jersey, states that 'The presence of *T. pisana* on a variety of erect plants . . . would seem to suggest that most emphasis should be given to their erect form', and he found *T. pisana* 'aestivating on tall plants including . . . fennel (*Foeniculum vulgare* Mill.) and nettles (*Urtica dioica*)'. Tall and erect vegetation is absent from the sites at St. Ives and as a result the snails have modified their behavioural pattern to suit the conditions imposed by the shorter vegetation, retiring to the base of the plants during the daytime. Here they can be found withdrawn into their shells protected in the cool shade, and without any trace of an epiphragm which is commonly seen in the snails at those colonies where aestivation takes place on the exposed stems of plants.

The second feature distinguishing the Cornish habitats is the complete absence of any pure sand within the areas colonized by *T. pisana*. Both in South Wales and the Channel Isles *T. pisana* is frequently settled in areas comprised essentially of sand-dunes, or in close proximity to them. Indeed Barrett (1972) states that in Guernsey at those places where the sand-dunes give way to the rocky headlands, so the colonies of *T. pisana* die out. Again, referring to the habitats in Jersey, Barrett (1975) comments 'where the sand itself showed a decline in shell content, *T. pisana* declined'. These observations contrast sharply with the situation at St. Ives, where the pure sand is replaced by a moderately sandy humus. These colonies are established on almost vertical banks of 'head', consisting essentially of boulder clay containing embedded angular rocks, portions of which are overlain by the sandy soil. This soil attains a depth of about 20 cm towards the bottom of the bank where it has gradually been washed down. Where *T. pisana* has the choice it evidently displays a preference to settle in those areas containing sand only, but the species is, nevertheless, demonstrably able to flourish on sites deficient in pure sand. At St. Ives a sufficient amount of wind blown sand, originating from the surrounding beaches, is deposited on the sites, maintaining the required calcareous level of the soil. Additionally, in common with other colonies of *T. pisana*, those found at St. Ives are associated with large numbers of *Cochlicella acuta* (Müller) and to a lesser extent *Candidula intersecta* (*Helicella caperata*) and *Cernuella virgata* (da Costa), which contribute to the calcareous make up of the soil with their deposits of dead shells. Even so the pH content at St. Ives, with its maximum of 7.5 pH, does not reach the level of 8 pH and over noted by Barrett (1972) in Guernsey.

Lack of sand at St. Ives may also account for the comparatively few records obtained relating to *T. pisana* burying itself in the soil. Although areas where the soil is sufficiently friable for this activity to occur do exist, particularly at the principal colony, it has only been observed infrequently and without any precise understanding of the factors causing it. It is suggested that more profitable studies concerning this habit could be carried out at those colonies established in the predominantly sandy areas occurring in Guernsey and elsewhere.

It is apparent from the evidence gathered to date that *T. pisana* will tolerate conditions far more exposed to the effects of the wind than had previously been expected (Turk 1966). The species will remain active with near gale force winds blowing across the sites, provided that the ameliorating effects of sufficient ground moisture are present. This agrees entirely with Barrett's (1972) finding, that *T. pisana* established in Guernsey on the wet west coast and without any protection other than that offered by the density

of the herbage, is able to survive in similar exposed conditions. Again, referring to Tenby, South Wales, Pitchford (*in litt.*, 26.XII.1974) remarks on the exposed position of the colonies there, and how on one occasion during a severe gale with winds reaching force 9, he observed *T. pisana* on the move and apparently unaffected by the strength of the gale.

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THE NON-MARINE MOLLUSCA OF COLONSAY AND ORONSAY

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(*Read before the Society, 15 May 1976*)

Abstract: Lists of land and freshwater Mollusca collected on Oronsay and Colonsay are presented together with locality and habitat information.

In August 1975 at the invitation of Dr. Paul Mellors, I visited Colonsay and Oronsay to collect first-hand the rich non-marine mollusc fauna of the mesolithic shell middens on the latter island and to use them to interpret ecological conditions at the time when the middens were occupied (*c.* 3500 B.C.). To further this study and to increase coverage of the Conchological Society's mapping scheme, I collected living non-marine molluscs on both islands. The two islands have only rarely been visited by malacologists. Musham (1916) includes the only published records of which I know, although there is an unpublished report of an Imperial College zoological expedition to Oronsay in 1956 which incidentally lists some non-marine molluscs. The entire vice-county of South Eubodes, which includes Islay, Jura, Colonsay, Oronsay and associated minor islands, is poorly recorded. In the 1951 census (Ellis 1951, p. 227) it shared with Aberdeen South the lowest total of any vice-county; 39 species and five doubtful records. By 1965, however, this total had been raised to 52 with 3 doubtful (Kerney 1966), but there were no post-1950 records for Colonsay and Oronsay in the Society's census notebooks prior to my visit.

My own modest collecting centred in two areas (Fig. 1): around Kiloran, Colonsay and between The Priory and Eilean Treadhrach, Oronsay. I visited as wide a range of habitats as possible and recorded 53 species, including several new vice-county records. The purpose of this note is to record the molluscs found and the habitats in which they occurred. To some extent the latter will provide a basis for interpretation of the subfossil faunas from the middens, if due allowance is made for subsequent man-made and natural changes in the islands.

LIST OF COLLECTING LOCALITIES

COLONSAY

1. Kiloran Bay. Rocky cliffs and short turf.
2. Kiloran Bay. (a) small stream with sandy bed; (b) sand dunes.
3. Kiloran Bay. Same stream further inland with good growth of aquatic vegetation.
4. Loch an Sgoltaire. Where tributary stream enters loch, rocky substrate.
5. Kiloran Farm. Old hazel coppice.
6. Colonsay House. (a) same stream as 2(a) and 3, pebbly substrate and no vegetation; (b) recent woodland with exotic plants; (c) garden of Kiloran Farm.
7. Near Kiloran Farm. (a) Millstream, rocky substrate; (b) adjacent roadside ditch with muddy substrate; (c) walls of ruined mill.
8. Loch Fada. Exposed shores with stony substrate and little weed in less than 30 cm water depth.
9. Beinn nam Fitheach. (a) mouth of small stream, sandy bottom; (b) ancient deciduous wood; (c) rocky shore with short turf and driftwood.
10. Scalasaig. Vegetated ditch below the War Memorial.

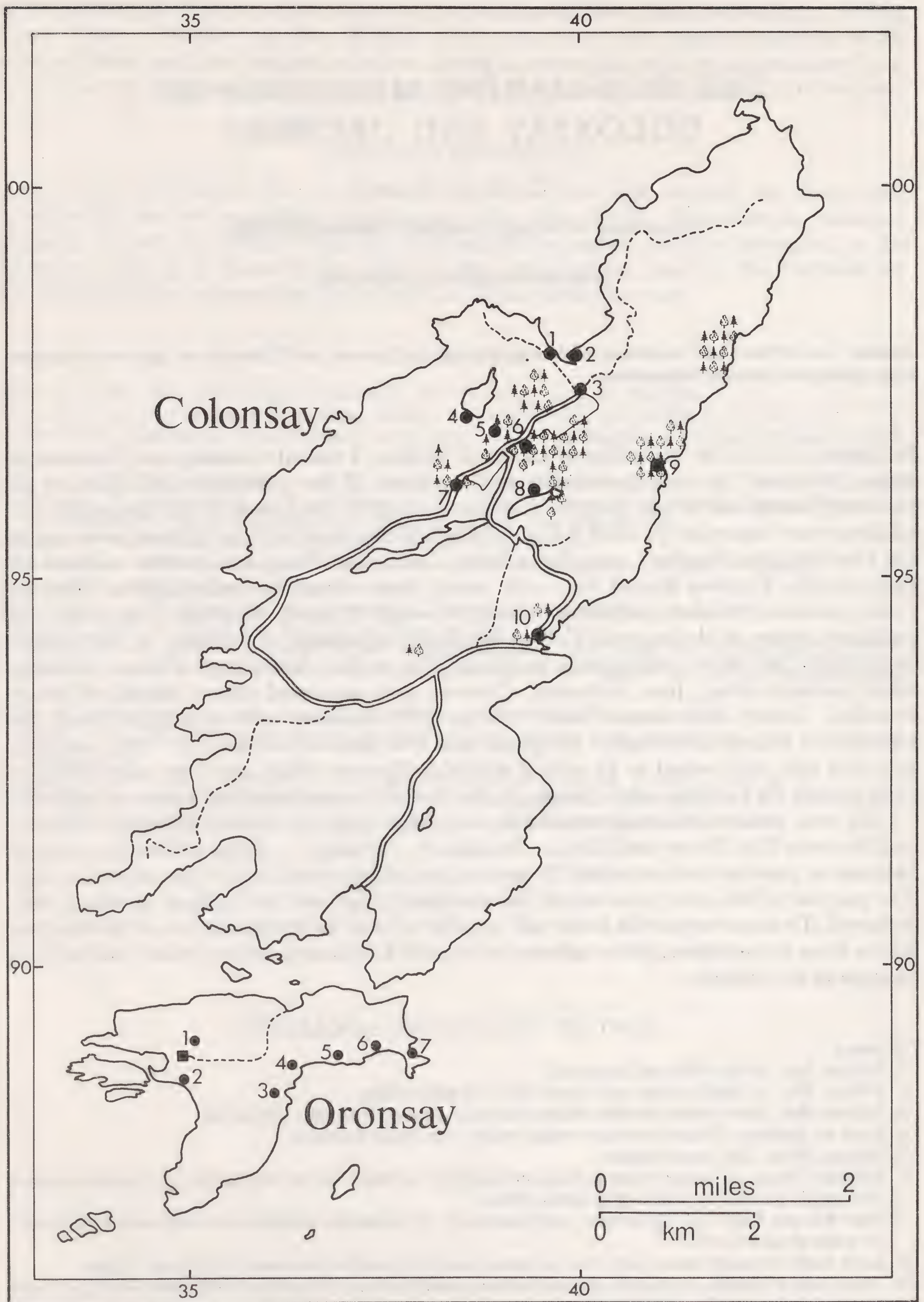


Fig. 1. Collecting sites in Colonsay and Oronsay.

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ORONSAY

- 1. The Priory. (a) vegetated ditch; (b) walls of ruined priory.
- 2. The Priory. Mouth of small stream, sandy substrate.
- 3. Near Seal Cottage. (a) spring, muddy with abundant vegetation; (b) wet flushes as (a); (c) shoreline shell sand under short turf; (d) walls of ruined cottage.
- 4. 'Cnoc Coig'. (a) shoreline with short turf; (b) under driftwood.
- 5. Cnoc Rearch. (a) shoreline with short turf; (b) under driftwood.
- 6. Cnoc Sligeach. (a) stream with sand and mud substrate and abundant vegetation; (b) under driftwood.
- 7. Opposite Eilean Treadhrach. Sand dunes.

TABLE 1
Land Molluscs of Colonsay and Oronsay

SPECIES	LOCALITIES											
	COLONSAY											
	Wood			Shore			Human					
	5	6b	9b	1	2b	9c	6c	7c				
<i>Carychium minimum</i> Müller	-	-	-	-	-	-	-	-	-	-	-	-
<i>Oxyloma pfeifferi</i> (Rossmässler)	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cochlicopa lubrica</i> (Müller)	-	-	-	L	-	L	L	-	-	-	-	-
<i>C. lubricella</i> (Porro)	-	-	-	-	-	-	-	-	-	L	L	L
<i>Columella aspera</i> Waldén	L	-	L	-	-	-	-	-	-	-	-	-
<i>Vertigo antivertigo</i> (Draparnaud)	-	-	-	-	-	-	-	-	-	-	-	-
<i>V. substriata</i> (Jeffreys)	-	-	-	-	-	-	-	-	-	L	-	-
<i>V. pygmaea</i> (Draparnaud)	-	-	-	-	-	-	-	-	-	-	L	-
<i>Leiostryla anglica</i> (Wood)	L	L	L	-	-	-	-	L	-	-	-	-
<i>Lauria cylindracea</i> (Da Costa)	-	L	-	L	-	-	L	L	-	-	-	L
<i>Vallonia excentrica</i> Sterki	-	-	-	-	-	-	-	-	-	L	-	L
<i>Acanthinula aculeata</i> (Müller)	-	-	L	-	-	-	-	-	-	-	-	-
<i>Spermodea lamellata</i> (Jeffreys)	L	-	L	-	-	-	-	-	-	-	-	-
<i>Punctum pygmaeum</i> (Draparnaud)	-	-	L	-	-	-	-	-	-	L	L	-
<i>Discus rotundatus</i> (Müller)	L	L	L	L	-	L	L	L	-	-	-	L
<i>Arion ater</i> (L.) agg.	-	-	-	-	L	L	-	-	-	-	-	L
<i>A. circumscriptus</i> Johnston	-	-	-	-	-	-	-	-	-	-	-	L
<i>A. cf. fasciatus</i> (Nilsson)	-	-	-	-	-	-	-	L	-	-	-	-
<i>A. intermedius</i> Normand	-	-	L	-	-	-	L	-	-	-	-	-
<i>Vitrina pellucida</i> (Müller)	L	-	-	-	-	-	-	-	-	L	d	d
<i>Vitrea crystallina</i> (Müller)	L	-	-	L	-	-	-	-	-	-	-	-
<i>V. contracta</i> (Westerlund)	-	L	-	-	-	-	-	-	-	L	L	-
<i>Nesovitrea hammonis</i> (Ström)	-	-	L	d	-	-	-	-	-	-	L	L
<i>Aegopinella pura</i> (Alder)	-	d	-	L	-	-	-	-	-	-	-	-
<i>A. nitidula</i> (Draparnaud)	L	-	-	L	-	-	-	-	-	-	-	-
<i>Oxychilus cellarius</i> (Müller)	-	-	-	d	-	-	L	-	-	-	-	L
<i>O. alliarius</i> (Miller)	L	L	L	d	-	-	L	L	-	-	L	L
<i>Zonitoides excavatus</i> (Alder)	-	-	L	-	-	-	-	-	-	-	-	-
<i>Milax sowerbyi</i> (Férussac)	-	-	-	-	-	-	L	-	-	-	-	-
<i>Limax maximus</i> L.	-	-	L	-	-	-	-	-	-	-	-	-
<i>L. marginatus</i> Müller	-	-	L	-	-	-	L	-	-	-	-	-
<i>Deroceras laeve</i> (Müller)	-	L	-	-	-	-	L	-	-	-	-	-
<i>D. reticulatum</i> (Müller)	-	-	-	-	-	L	L	L	-	-	-	L
<i>D. caruanae</i> Auctt.	-	L	-	-	-	-	L	-	-	-	L	-
<i>Euconulus fulvus</i> (Müller)	-	L	L	-	-	-	-	-	-	-	-	-
<i>E. alderi</i> (Gray)	-	-	-	-	-	-	-	-	-	-	-	-
<i>Clausilia bidentata</i> (Ström)	-	L	-	L	-	L	L	-	-	-	-	-
<i>Balea perversa</i> (L.)	-	-	L	-	-	-	L	L	-	-	-	L
<i>Helicella itala</i> (L.)	-	-	-	-	L	-	-	-	-	L	L	-
<i>Cochlicella acuta</i> (Müller)	-	-	-	-	L	-	-	-	-	L	L	-
<i>Ashfordia granulata</i> (Alder)	-	-	-	L	-	-	L	L	-	-	-	-
<i>Trichia hispida</i> (L.)	-	-	-	-	-	-	L	-	-	-	-	L
<i>Cepaea nemoralis</i> (L.)	-	-	-	L	L	L	L	-	-	L	L	-
<i>C. hortensis</i> (Müller)	-	-	-	L	-	-	-	-	-	d	d	-
<i>Helix aspersa</i> Müller	-	-	-	-	-	-	-	-	-	-	-	L

TABLE 2

Freshwater molluscs of Colonsay and Oronsay

SPECIES	LOCALITIES														
	COLONSAY										ORONSAY				
	2a	3	4	6a	7a	7b	8	9a	10		1a	2	3a	3b	6c
<i>Potamopyrgus jenkinsi</i> (E. A. Smith)	—	L	—	L	—	—	L	—	L		—	—	—	—	—
<i>Lymnaea truncatula</i> (Müller)	—	—	—	—	—	—	—	—	—		—	—	—	L	—
<i>L. peregra</i> (Müller)	L	—	L	—	—	—	L	d	—		—	L	L	—	L
<i>Anisus leucostoma</i> (Millet)	—	—	—	—	—	—	—	—	—		—	—	—	—	L
<i>Ancylus fluviatilis</i> Müller	—	—	L	—	L	—	—	—	—		—	—	—	—	—
<i>Sphaerium corneum</i> (L.)	—	—	—	—	—	—	L	—	—		—	—	—	—	—
<i>Pisidium casertanum</i> (Poli)	—	—	—	—	—	L	—	—	—		—	—	L	L	—
<i>Pisidium personatum</i> Malm	—	—	—	—	—	—	L	—	—		L	—	—	L	—

L = live

d = dead shells only

DISCUSSION

Fossil samples so far examined include five additional species not yet found alive on either island. These are *Carychium tridentatum* (Risso), *Columella edentula* (Draparnaud), *Vertigo pusilla* Müller, *Pupilla muscorum* (L.) and *Vallonia costata* (Müller). All five could possibly still survive on the islands, although *Vertigo pusilla*, in particular, was formerly much more widespread than at present. Both column samples that I have examined from two separate middens include woodland species in small numbers throughout. At present Oronsay has no woodland and very few trees. The presence of *Acanthinula aculeata*, *Leiostryla anglica* and *Euconulus fulvus* in the middens strongly suggests that at the time of occupation Oronsay was covered with woodland, or at least scrubby bush.

One or two species call for comment. The specimens of *Euconulus alderi* represent the most northerly record for the segregate so far. The little available information on the distribution of the segregates of *Euconulus* in Britain indicates that *E. alderi* becomes progressively rarer northwards. Both *E. fulvus* and *E. alderi* occurred in typical habitats; woodland for the former and marsh for the latter.

Deroceras caruanae auctt. is presumably a relatively recent introduction. On Colonsay it was only found near human settlement, but a single example was taken on Oronsay, under driftwood well away from the nearest habitation. Being frost-free, the islands form a suitable habitat for this Mediterranean slug.

A single example of *Acanthinula aculeata*, a persistent, though rare, woodland indicator throughout the midden samples, was found under a hazel bush in ancient woodland on the slopes of Beinn-nam-Fitheach. Almost certainly this species has been restricted by clearance of woodland and bushes on both islands. Possibly *Columella edentula* and *Carychium tridentatum* have also been restricted in this way. All *Columella* seen were *C. aspera*. Certainly clearance seems to have altered Oronsay drastically since the middens were occupied.

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SOME ASPECTS OF GROWTH AND DEVELOPMENT IN THE RIVER LIMPET, *ANCYLUS FLUVIATILIS* (GASTROPODA: ANCYLIDAE)

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(Read before the Society, 15 May 1976)

Abstract: Running-water *Ancylus fluviatilis* eggs laid in March and July were allowed to develop in laboratory standing-water culture tanks and data collected on their subsequent development. Growth curves for height, length and width closely resembled each other, all following a double sigmoid growth curve. The curve for length was similar to that for aperture length of running-water *Ancylus fluviatilis* (Hunter 1961b). Data collected on the egg development proved similar to those of previous workers, except that more eggs were laid than hatched from the egg capsules. Sedimentation affects development of eggs and young limpets and may be a controlling influence on limpet distribution. The maximum sizes attained by laboratory individuals were less than those for samples collected from river and standing water, however they copulated and laid viable eggs at these lower dimensions.

Growth in freshwater pulmonate gastropods has been observed and described by numerous authors. For example, Turner (1926), Crabb (1929), Baily (1931), Imai (1937) and Berrie (1965, 1966) have studied *Lymnaea* species; De Wit (1955) *Physa fontinalis* (L.) and *P. gyrina* Say; and Calow (1973b) *Bathyomphalus contortus* (L.). The pattern of growth and development in *Ancylus fluviatilis* has been studied by Hunter (1953, 1961a,b), Geldiay (1956), Maitland (1965) and Durrant (1975), with aspects of egg pod structure described by Bondesen (1950a). Distribution and ecology were discussed by Boycott (1936) and the correlations between development, life history and ecology of *Ancylus fluviatilis* are described by Macan (1963, 1972) and Calow (1973a, 1974a,b).

Ancylus fluviatilis is an annual (Hunter 1953). It grows rapidly after emergence in March/April or June/July, virtually ceases to grow in winter, resuming growth in the spring, after which growth continues slowly through oviposition up to death in June or July. Some individuals have been described in the September of the same year as they breed (Hunter 1961a) and large, old, weak forms (length 8.40 mm) were collected in Lake Windermere in mid-October 1975. These were confined to deeper water and sheltered rock crevices. The double sigmoid growth curve found in the river limpet seems to be typical of temperate freshwater pulmonates (Hunter 1961a).

METHOD OF STUDY

In March 1974 stones containing egg capsules of *Ancylus fluviatilis* were collected from the river Lea, Hertford. These were placed in an aerated aquarium in an unheated stock room, so duplicating the natural conditions as nearly as possible. The development of the pods was observed and twenty newly hatched spats were measured immediately after emergence for height (using a micrometer to an accuracy of 0.01 mm), width and length (measured to an accuracy of 0.05 mm, using a millimetre graticule and a binocular microscope). Within three weeks large numbers of spats had hatched. One hundred of these were removed from the stock tank, which was cleaned out, and all

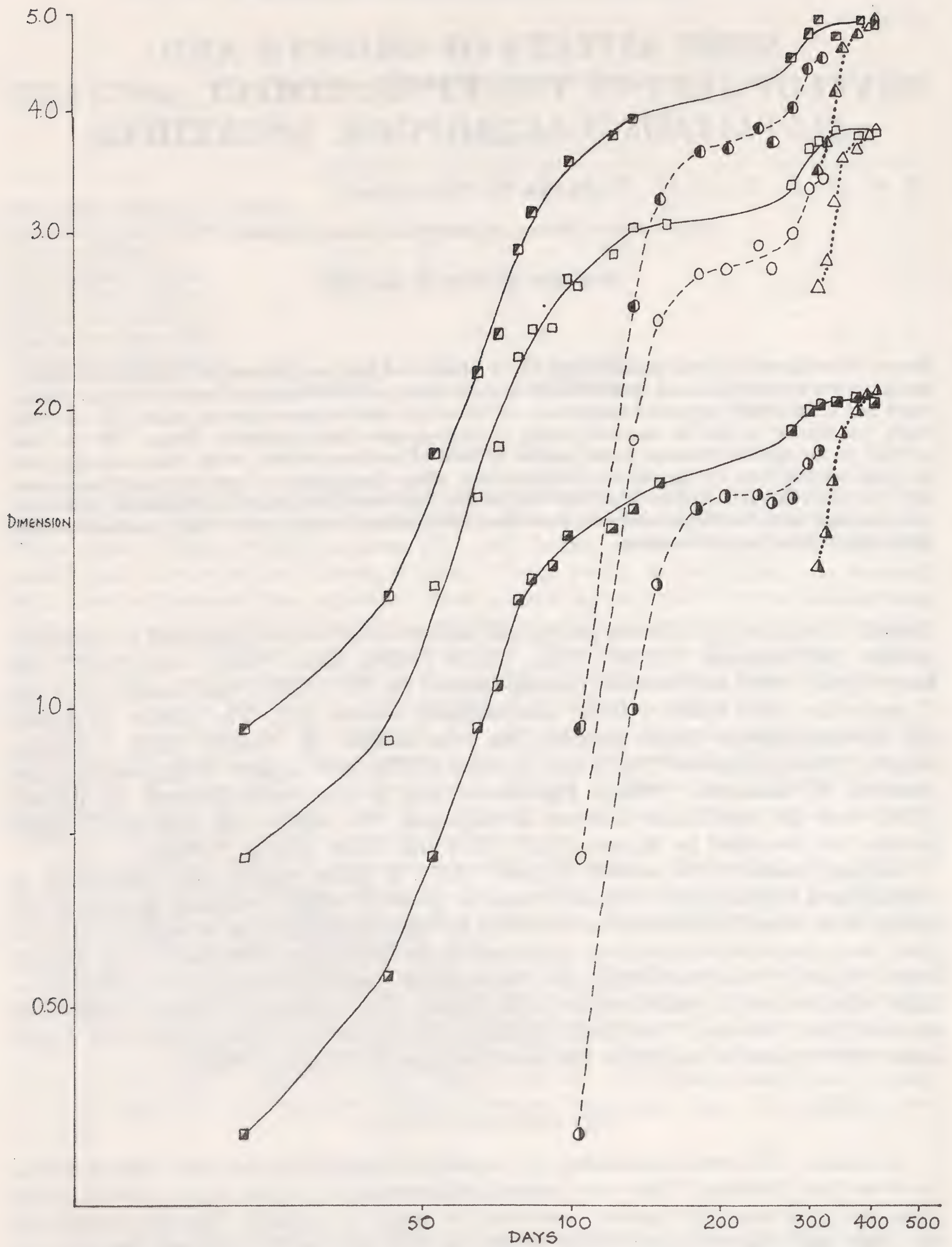


Fig. 1. Growth curves for height, width and length of laboratory cultured *Ancyclus fluviatilis*

Sample S ————— Sample J - - - - - Sample F

■ length ● length ▲ length
 □ width ○ width △ width
 ▣ height ● height ▴ height

undeveloped egg pods and unwanted spats removed. The spats were then replaced along with water and washed, clean stones from the river. This stock tank was labelled sample S. The growth and development of these limpets was closely monitored by measuring at regular intervals the height, width and length of the largest fifteen. This often involved measuring almost half the stock and using the largest for statistical analysis. The curve produced (Fig. 1) is equivalent to the 'mass curve' of Medawar (1945) in which each point represents the mean size of the largest 15 individuals taken at any particular time. The survey continued until May 1975 when mature individuals began to die. During February 1975, fifteen individuals of a small size class (between length 3.1–4.0 mm) were removed from the stock tank, measured and placed in a separate culture tank. The growth of this sample (F) was closely followed until their death in June 1975.

Eggs were also collected from the river Lea in July 1974. These were allowed to hatch (July 1974) and thirty spats were cultured. The growth of these (sample J) was studied until the population died out in February 1975.

RESULTS

TABLE 1

Overall dimensions of sampled limpets (mm)

	HEIGHT (H)			WIDTH (W)			LENGTH (L)		
	\bar{H}	S_H	RANGE	\bar{W}	S_W	RANGE	\bar{L}	S_L	RANGE
Hatching	0.37	0.04	0.32–0.45	0.70	0.06	0.60–0.75	0.93	0.09	0.75–1.00
1 year (S & F)	2.07	0.14	0.73–2.35	3.90	0.32	1.30–4.70	5.00	0.36	1.80–5.80
River			2.30–3.65			3.70–7.00	7.00	1.07	4.90–11.20

River sample taken from a similar region of the river Lea as the original eggs of S sample. Standard symbols for mean \bar{H} , standard deviation S_H etc.

TABLE 2

Egg capsule data

	N	S_N	RANGE	GELDIAY (1956) range	BONDESEN (1950) range	HUNTER (1953)
Eggs per pod at oviposition	7.0	1.10	1.00–9.00	0–11 mean	up to 10	
Eggs hatching per pod	4.1	1.00	1.00–7.00	3.99 (4.27 in lab.)		
Mean dimensions of capsule (mm)			2.50–3.20	2.70–3.42	2.80–3.30	
Egg size (mm)			1.20–2.00 × 0.50–1.50	1.38 × 1.23	1.20 × 1.42	1.30 diam.
Egg cell size (mm)			0.10–0.20			
Hatching time (days)			19–28			25
Egg capsules laid per limpet			up to 8	10–20	4–7	12
Frequency of eggs hatching per capsule	NUMBER OF EGGS HATCHING			0 1 2 3 4 5 6 7		
	NUMBER OF CAPSULES			– 1 2 10 22 17 1 1		

TABLE 3

SITE	Mean increase in length (mm) per 10 days		
	WINTER	SPRING	SUMMER
Upper Craigton Burn (Hunter)	0.09	0.22	
S	0.05 (Sept.-Jan.)	0.15 (Jan.-March)	0.26 (May-August)
J	0.05 (Nov.-Jan.)	0.18 (Jan.-Feb.)	0.31 (July-Sept.)
F		0.16 (Feb.-May)	

Tanks containing samples S, F and J had their water changed regularly and the specimens were occasionally transferred to other aquaria pre-cultured with algae. The temperatures were taken each time the limpets were measured and averaged 15.5–19.0°C except for the period late October to mid-January when temperatures varied between 12.0–14.0°C. Although these temperatures were not identical to the natural environmental conditions which were 2–3°C lower, they follow a similar trend (Geldiay 1956).

Egg capsules produced by samples S and F in April 1975 were observed and some data collected.

Table 1 shows some of the dimensions of sampled limpets and Table 2 some information of egg pods with the seasonal growth of limpets in Table 3. Appendix A contains the mean shell length at each sampling interval for each limpet series. Fig. 1 illustrates the growth curves for height, width and length (respectively equivalent to shell height, aperture breadth and aperture length of Hunter 1961a) for samples S, F and J plotted as a log \times log graph of dimension against time. Fig. 2 is of a typical newly laid egg capsule.

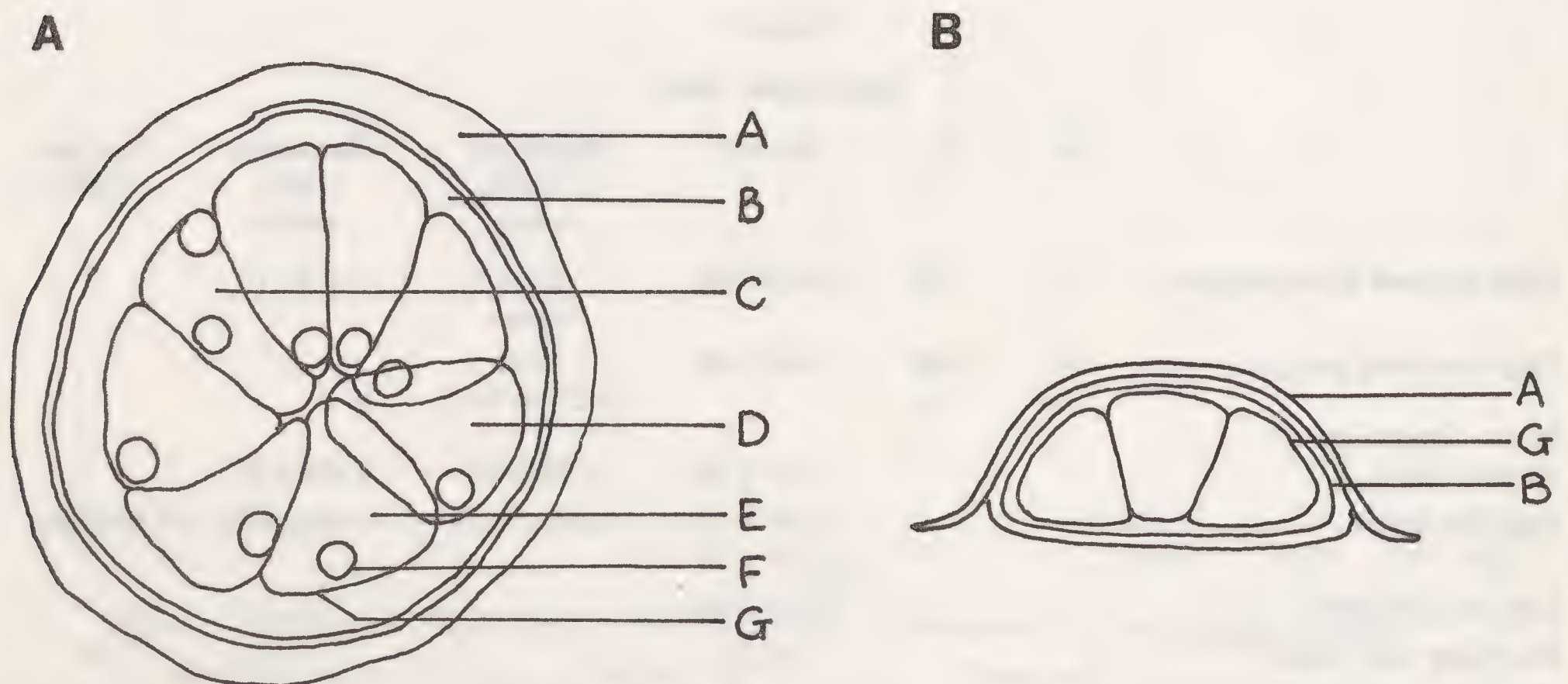


Fig. 2. A A newly laid egg capsule of *Ancylus fluviatilis*. A—external capsule, B—internal capsule, C—egg with two egg cells, D—first egg laid, E—perivitelline fluid, F—egg cell and G—egg membrane.
B Section through an egg capsule.

DISCUSSION

Eggs and development. The spat size at hatching (Table 1) compares favourably with results by Hunter (1953) where the mean shell length at hatching was 1.05 mm. The duration of development from egg laying to hatching is also similar, but the maximum size reached by laboratory limpets was considerably lower than for comparable river forms (Table 1). Hunter (1953), Geldiay (1956) and De Wit (1955) all found that the individual shell dimensions of breeding populations fluctuated from year to year and from individual to individual within each year. Calow (1973a) suggests variations in diet may affect growth and presents evidence to suggest that a lichenophilous habit may result in reduced growth. Schmid (1932) indicated a lichen food preference in *Ancylus fluviatilis*. No lichen growth was observed in the tanks but food supplies may have had some limiting influence on growth especially in winter. Hunter (1953) showed that limpets grown on the more natural stone environment grew faster than those growing on the sides of glass jars. The length of sample S spat (Appendix A) after forty days was 2.19 mm. Hunter's figure of 2.10 mm for limpets on glass is closely comparable (although there may be a leeway in the number of days from hatching). However, limpets living on stone grew to a length of 2.79 mm in the same period, a difference of 0.6 mm in approximately 3.0 mm growth. These differences projected forward to the mean size reached by river forms (i.e. 6.0 mm length) would account for some 1.0–1.5 mm extra growth in river forms and gives some credence to the size discrepancy between laboratory and natural growth. In measuring samples S, J and F no discrimination was made between those grazing on stones and those living on the sides of the aquaria. This size difference probably arose during the winter months when river forms grew almost twice as fast as the laboratory culture (Table 3).

Oviposition. The numbers of eggs per capsule are given in Table 2. The number hatching is similar to Geldiay (1956) and Hunter (1953). However, it was noticed that egg pods contained more eggs at oviposition than hatched, and the abortion of some of these was noticeable in the first week. Table 2 shows a 41.4% mortality rate of limpets in the egg capsule. The ratio of eggs laid per adult (47:1 Hunter 1961a) in *Ancylus fluviatilis*, although still much lower than other pulmonates, may not be quite as low as previously forecast. The number of eggs per capsule was 1–9, but egg pods containing only one or two eggs were often produced by individuals which were at the end of their egg laying activity. Some of these egg capsules, unlike the others, were not secured to the sides of aquaria or the smooth undersides of stones (Calow 1974a, Geldiay 1956), but were free, lying at the bottom of the culture tank. Egg pods which accumulated detritus or had algal growth on their surfaces seldom produced viable spats. This may well explain why eggs are laid on the undersurface of stones where sedimentation and algae are at a minimum. Detritus cover on stones could be a limiting factor in the early development of *Ancylus fluviatilis*, so restricting the invasion or repopulation of areas of high sedimentation.

Often eggs within the egg capsules had two egg cells (Bondesen 1950b) and Fig. 2. The egg size was also variable, Table 2; some of them could be classed as dwarf eggs (Bondesen 1950b).

Individual growth. The growth curves for length are very similar to that shown for river *Ancylus fluviatilis* (Hunter 1961b). Growth is at a maximum in May–June and January–February in sample S and July–August and January–February for sample J. The greater growth is in the summer, with the growth rate per ten days slightly more in summer and the winter growth half that found by Hunter (1953) (Table 3). In 1975 winter growth reduction started in September–October and is similar to *Ancylus fluviatilis* from Lake

Windermere (Geldiay 1956). Table 3 also differentiates between spring and summer growth, summer being the greater. The overall association between each shell dimension under these standing-water conditions seems to be isometric, as each dimension follows a similar trend (Fig. 1).

The number of individuals in each culture tank was assessed only in samples J and F. Over the winter period a fifty per cent reduction in sample J occurred, whereas in sample F all individuals remained viable until June. This fact may point to winter being an environmentally vulnerable period in the life cycle of *Ancylus fluviatilis* (Hunter 1953, 1961a).

In the confines of the enclosed tank observations suggest that the size distribution of individual limpets remained fairly constant. Those that develop first seem to maintain their initial size increase throughout the year, some after one year's growth were only 1.8 mm long (Table 1). The rapid development of transferred individuals in sample F seems to suggest a constraining influence by the larger limpets on the development of smaller forms perhaps due to inadequate food supply. A similar occurrence in the development and hatching of *Ancylus fluviatilis* eggs is described by Maitland (1965).

Laboratory limpets copulated in March and started to lay eggs early in April through to mid-May. The eggs started hatching at the end of April and early May. Samples from the river Lea (from the same site as the original collection and so assumed to be from the same filial generation) did not show egg pods until late April and early May (copulation was observed in mid-April) some two weeks later than the laboratory forms although their length was considerably greater (Table 1).

No chain copulation (Geldiay 1956) was observed in either tanks or in the river Lea, but perhaps the density of individuals was not so great as in Lake Windermere.

In the laboratory, specimens as small as 4.0 mm in length had active ovotestis and laid egg capsules producing viable spats. The river *Ancylus fluviatilis* were 4.0 mm in length in February 1975, but showed no sexual maturity until April and May (warmer spring conditions). This association of sexual maturity with suitable environmental conditions is also shown by Lake Windermere *Ancylus fluviatilis* (length 5.0 mm) which were copulating and egg-laying in October 1975, the same year as they hatched.

The cultured limpets died in June, at which time their shells were well coated with algae and detritus, whereas river forms may continue to lay eggs into July and survive to October.

The infestation of *Ancylus fluviatilis*, in the culture tanks, by *Chaetogaster limnaei* Von Baer increased with the age of the limpets. Quite large numbers of the oligochaetes were found on and in the organ systems of dead limpets left decomposing in the culture tanks.

ACKNOWLEDGMENT

I should like to thank Peter Bray for his help in the analysis of the data and to my wife for her assistance in the typing of this paper.

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APPENDIX A

Mean shell length (L) in mm at each sampling time for each sample

DATE 1974	S SAMPLE		J SAMPLE		F SAMPLE	
	\bar{L}	S_L	\bar{L}	S_L	\bar{L}	S_L
April 22	0.95	0.09				
May 13	1.30	0.18				
June 4	2.19	0.41				
June 17	2.90	0.41				
July 8	3.56	0.65	Hatched mid-July			
August 13	3.91	0.47	2.53	0.26		
September 10	3.43	0.54	3.28	0.45		
September 26	—		3.64	0.37		
November 5	—		3.73	0.30		
November 27	3.52	0.37	3.85	0.57		
1975						
January 6	4.52	0.18	4.03	0.28		
January 28	4.80	0.18	4.42	0.35		
February 13	4.94	0.32	4.50	0.32	3.45	0.29
March 13	4.75	0.15	died out		4.65	0.32
April 14	4.96	0.15			4.79	0.41
May 13	4.92	0.05			4.96	0.34
June 3	—				4.94	0.36

Symbols as in Table 1.—no recorded result.

BALANCE SHEET AS AT 31st DECEMBER, 1975

	£	£	£
Fees and Subscriptions in Advance ...		405.03	710.68
Life Membership Fund ...		1,530.00	786.08
Reserve and Research Fund ...		1,209.97	
			1,436.94
			<u>2,933.70</u>
<i>Capital Account</i>			
Balance Brought Forward ...	5,625.87		
Less Loss on Revaluation of Mersey Docks and Harbour Board Stock	236.68		344.00
	<u>5,389.19</u>		222.09
Add Surplus for the Year ...	525.15		721.52
	<u>5,914.34</u>		
			1,522.06
			400.00
			769.20
			892.95
			753.82
			<u>500.00</u>
			6,125.64
			<u>£9,059.34</u>

L. LLOYD-EVANS } *Hon. Auditors.*
WM. F. EDWARDS } 24.2.1976

10th February, 1976.
P.G.

MARJORIE FOGAN,
Hon. Treasurer.

PROCEEDINGS OF THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND

TREASURER'S REPORT, 1975

As all Members are aware, it has unfortunately been necessary to increase the Annual Subscription, which is now £5.00 for Ordinary Members, £6.00 for Family Membership and £1.00 for Junior Members. To encourage prompt payment and to avoid the considerable cost of individual reminders, Ordinary and Family Members may deduct the sum of 50p from these if paid before 31st March.

The increase can hardly come as a surprise in the present inflationary conditions and has indeed been under consideration for some time. Your Council are disappointed that the increase has coincided with the Society's Centenary Year. It had been hoped that this might have been avoided, but it was impossible to envisage two large postal increases within the year, nor that a very considerable increase in printing costs would raise the price of the most recent *Journal* part to such a high level. These factors necessitated the holding of a Special General Meeting to increase subscription rates for 1976.

The Society's income shows increases in Members' subscriptions, Subscribers' payments, sales and interest on investments by comparison with 1974, but these have not been sufficient to keep pace with inflation. The substantial surplus shown in the Balance Sheet is a result of two additions to receipts which are unlikely to recur. By a happy chance a last portion of the Society's library (the rest of which was sold more than twenty years ago) was discovered in the form of a collection of papers of the Palaeontographical Society which had been on loan for the whole of this time. These papers were sold for £360; the sum was made up to the minimum of £500 and has been invested in Manchester Corporation 13½% Loan. The Life Members' Fund has also been greatly increased by the addition of 13 new Life Members (including two pairs of Family Life Members) whose subscriptions amounted to £680, which will be invested. It will be seen that without these increments, instead of a surplus, there would have been a substantial deficit for the year.

An investment account has been opened with the P.O. Savings Bank, and a large portion of funds held in the bank deposit account have been transferred to this to take advantage of the more favourable interest rate.

25 Members and 2 Junior Members are in arrears with 1975 subscriptions. All Members are reminded that no further publications for 1976 will be sent to Members whose current subscriptions are unpaid; any publications withheld will be sent on receipt of the arrears.

MARJORIE FOGAN,
Hon. Treasurer.

REPORT OF THE COUNCIL 1975-76

Membership. It is with deep regret that the Society has to report the deaths of the following Members:—Miss K. M. Morehouse 1969-75, Mr. G. Eastwood 1967-73, Mr. C. A. Raffray 1951-75 and Mr. A. E. le Gros 1972-76. Total membership now stands at 588, comprised of the following categories:—Full Members 484, Family Members 29, Family Life Members 5, Life Members 27, Honorary Members 1, Junior Members 42.

During the year 65 new Members were elected, 18 of whom were juniors. 30 Members resigned from the Society, 7 Juniors, and 30 Members were removed for non-payment of subscriptions, of these 11 were juniors. It is encouraging to note that despite the increase in subscription rates in January 1976, membership has not decreased.

Subscribers. In 1975 the number of subscriptions to *Journal of Conchology* increased by 2, reaching a total of 170. This includes 6 cancellations and 8 new subscriptions. Subscriptions to the *Conchologists' Newsletter* fell from 12 to 11.

Meetings. Eight ordinary, one annual general and one special general meeting were held in the Conversazione Room at the British Museum (Natural History) as follows:—15 March 1975: Lecture 'Diving for nudibranchs' by Dr. T. E. Thompson. 19 April 1975: Conversazione meeting. 17 May 1975: Lecture 'Conchological books' by T. Pain and P. Oliver. 18 October 1975: Lecture 'Grassland faunas' by Dr. J. Evans. 15 November 1975: Lecture 'Problems of photographing molluscs by an amateur' by D. G. Rands. A special general meeting to raise subscription rates was held prior to the ordinary meeting. 13 December 1975: Lecture 'Land molluscs of Victoria, S.E. Australia' by D. C. Long. 17 January 1976: Lecture 'Shells are for everyone' by S. P. Dance. 21 February 1976: Lecture 'Settlement of prosobranch larvae from the plankton' by Dr. V. Fretter. 13 March 1976: Annual General meeting: Presidential Address 'Marine Mollusca in Wales'.

PROCEEDINGS

Field meetings. Ten field meetings were held during 1975 as follows:—4–7 April: Herm, Channel Isles. 20 April: Grand Union Canal, Tring, Herts. 18 May: Braunston, Northamptonshire (joint meeting with the Northamptonshire Natural History Society). 7 June: Leicestershire. 21 June: Althorne, Essex. 6 July: Sandwich, Kent (joint meeting with the Kent Field Club). 9 August: Folkestone and Hythe, Kent. 13–14 September: Gedgrave, Suffolk (joint meeting with the Geological Society of Norfolk, the Ipswich Geological Group and the Tertiary Research Group). 26–28 September: Gower, South Wales. 19 October: Newbury, Berks.

Thanks are due to the following for leading these meetings:—Dr. J. E. Chatfield, Mrs. E. B. Rands, Mrs. C. J. Pain, Dr. T. E. Thompson, and Messrs. B. W. Barrett, A. G. Osborn, I. M. Evans, D. R. Worth, M. R. Block and R. A. D. Markham.

Three additional meetings were arranged especially for Junior members and more are planned for the forthcoming year.

Publications. Two parts of the *Journal of Conchology* were issued, vol. 28 parts 5 and 6. The latter concluded vol. 28 and included the title page and index for the volume. Quarterly 'Conchologists' Newsletters', an annual membership list and the centenary year programme of meetings, were also published.

RECORDER'S REPORT: NON-MARINE MOLLUSCA

A. 10-KILOMETRE SQUARE MAPPING

Work on preparing the maps for the *Atlas of non-marine Mollusca of the British Isles* is now almost complete. The atlas should be published in 1976, appropriately coinciding with the Society's centenary.

B. VICE-COUNTY RECORDS

The following new records have been verified since the last Recorder's report (*J. Conch., Lond.* **28**: 390). Unless stated otherwise, the date of collection was 1975.

Channel Isles (0, or 113): *Helicodiscus* cf. *singleyanus*, St. Ouen, Jersey (WV 55), J. Renouf; *Boettgerilla pallens*, St. Martin, Jersey (WV 6953), G. E. H. Long.

Cornwall West (1): *Boettgerilla pallens*, Reskadinnick (10/6341; garden), Mrs. S. M. Turk.

Devon South (3): *Cochlicella barbara*, Torquay (20/96), E. O. Bishop.

Somerset North (6): *Pisidium tenuilineatum*, R. Frome, Freshford (31/9363), B. Verdcourt.

Isle of Wight (10): *Acicula fusca*, St. Lawrence (40/5476), R. C. Preece.

Northampton (32): *Gyraulus laevis*, Althorp Park (42/6865), M. R. Wallis; *Deroceras caruanae*, Barby (42/5270), A. J. Rundle.

Monmouth (35): *Pisidium pseudosphaerium*, Magor (31/4286), M. Wade.

Worcester (37): *Bithynia leachii*, Worcester (32/8555; canal), E. O. Bishop.

Glamorgan (41): *Boettgerilla pallens*, St. Fagans (31/1177), D. C. Long.

Radnor (43): *Lymnaea auricularia*, R. Wye, Hay-on-Wye (32/24), S. P. Dance.

Cardigan (46): *Helicodiscus* cf. *singleyanus*, Machynlleth (22/69), Mrs. C. Trew and Dr. June Chatfield.

Montgomery (47): *Margaritifera margaritifera*, R. Vyrnwy, Meifod (33/11), Lord Cranbrook.

Flint (51): *Pisidium lilljeborgii*, Llyn Helyg (33/1177), Mrs. M. Fogan.

Cheviot (68): *Vertigo substriata*, Twizell House (46/1228), B. Colville.

Westmorland (69): *Deroceras agreste*, Grange Scar, Sunbiggin (35/6809), B. Colville.

Isle of Man (71): *Vertigo pusilla*, Castletown (24/26), R. Cairns, *ca.* 1890 (British Museum).

Aberdeen North (93): *Trichia striolata*, *T. hispida*, *Helix aspersa*, Rosehearty Links (38/9467), E. Kellock.

South Ebudes (102): *Vertigo antivertigo*, Oronsay (16/3688); *Acanthinula aculeata*, *Punctum pygmaeum*, Colonsay (16/4196), C. R. C. Paul. (See *J. Conch., Lond.* **29**: 107).

Ross West (105): *Deroceras agreste*, Achiltabuie (29/0109), B. Colville.

Sutherland East (107): *Deroceras caruanae*, *Monacha cantiana*, Golspie (28/8501; railway embankment), G. Osborn.

Sutherland West (108): *Zonitoides excavatus*, by Loch Loyal (29/6150); *Limax cinereoniger*, by Loch Hope (29/4755); *Deroceras caruanae*, Durness (29/3866), G. Osborn; *Milax sowerbyi*, *Limax maximus*, Inchnadamph (29/2521; garden), B. Colville.

Tyrone (H 36): *Aplexa hypnorum*, by Blackwater River (H 8861), R. Anderson.

The year has seen two additions to the British List. The first is *Helicodiscus* cf. *singleyanus* (Pilsbry), a small endodontid snail originally described from North America. In 1948 it was detected by Mr. J. G. J. Kuiper in Holland and in Switzerland (*Basteria*, **13** (1949): 40; *Archiv. Molluskenk.* **85** (1956): 163) and it has since been found in about a score of European localities. Little is known about its mode of life; most occurrences (both in Europe and North America) are dead shells, and several authors have suggested that the species

may be subterranean. At Machynlleth a single fairly fresh immature shell was sieved from leaf-litter in a moist mixed deciduous/coniferous wood. At St. Ouen three juveniles were recovered supposedly stratified 2 ft down in an archaeological excavation, but their condition appears fresh. It is not yet possible to say whether any of these shells belong to the supposed subspecies (or possibly distinct species) *inermis* Baker, to which most other European finds have been referred (see Pilsbry, *Land Mollusca of North America*, 2 (1948): 637).

The second new British find of 1975 is *Cochlicella barbara* (L.) (= *C. ventricosa* (Draparnaud); *C. ventrosa* (Férussac)). The colony at Torquay is on a calcareous grassy roadbank. Although apparently of limited extent, it has clearly been there for some years, as both freshly dead shells from the previous summer and old bleached specimens plugged with hardened soil occurred. How this Mediterranean snail reached Devon is unknown, but it may not be a coincidence that the Torquay area is noted for other introduced helicids (*Hygromia limbata*, *H. cinctella*). Elsewhere in northern Europe *C. barbara* is said to be established along a short stretch of the Channel coast on the frontier of France and Belgium, between Gravelines and La Panne.

The precise sites for these possibly rare new British species are for the moment being kept secret.

Boettgerilla pallens, first discovered in Britain in 1972 (*J. Conch.*, Lond. 28: 203), is recorded from three additional localities, all in the west, and is also known from a hothouse at Mickwell Brow, Wirral, Cheshire. Probably it is spreading, as in other European countries.

M. P. KERNEY

RECORDER'S REPORT: MARINE MOLLUSCA

Recording has continued this year with usual enthusiasm. Most new records from the Areas have come as the result of detailed investigations rather than casual visits. However, a great deal of very important background work which cannot be reported here has taken place. Many Area Representatives have shown marked improvement in the coastal recording by 10 km square. There can never be too much of this work as it is only in this way that a really definitive distributional pattern can be built up as the foundation of an Atlas. The group of Mollusca showing the greatest improvement in recording is the opisthobranchs which account for $\frac{2}{3}$ of the new Area records. This is largely due to the present interest in nudibranchs.

There are 154 new Area records and about 160 upgraded Area records. In addition there are at least 1,000 new 10 km square records. This is a splendid achievement, but it shows that we are still far from the point at which diminishing returns will reveal that most of the baseline information has been discovered.

RECORDS FROM THE AREAS

Unless otherwise stated, all records are of live animals. In the interests of brevity, and to reduce costs, only essential information can be shown here.

Shetland (1): *Mangelia attenuata*, *Nassarius incrassatus*, *Trophon muricatus*, *Diaphana minuta*, *Eulimella gracilis*, *Chlamys varia*, *Spisula elliptica*. Dead shells only, dredged from Sullom Voe in April 1975 (D. W. McKay). The last has not been checked. The same dredging upgraded 6 species and 16 more species (dead shells) were recorded for the first time this century.

Sutherland (2): This year has seen improvement in both coastal and offshore recording, due to the efforts of D. Adamson, R. Bremner, D. W. McKay, R. G. Meiklejohn and I. F. Smith. *Acanthochitona crinitus* Thurso Bay, 22.7.1975 (R.G.M.); *Littorina neglecta* Port Nancon, 4.7.1975 (R.G.M.); *Lora turricula* 58°53'N 10°50'W, 7.5.1975 (R.B.); *Simnea patula* 58°57'N 03°58'W, 18.5.1975 (R.B.); *Skeneopsis planorbis* Thurso Bay, 20.4.1975 (R.G.M.); *Limapontia coxsi* (*Acteonia senestra*) Balnakeil Bay, 12.7.1975 (I.F.S.); *Adalaria proxima* and *Aegires punctilucens* Port Nancon, 10.7.1975 (I.F.S.); *Ancula cristata* Balnakeil Bay, 12.7.1975 (I.F.S.); *Clione limacina* N.W. of Cape Wrath, 1974 (D. W. McK.); *Facelina auriculata* Thurso Bay, 6.4.1975 (R.G.M.); *Favorinus branchialis* Port Nancon, 10.7.1975 (I.F.S.); *Jorunna tomentosa* Balnakeil Bay, 12.7.1975 (I.F.S.); *Menestho divisa* Loch Eriboll, 3.7.1975 (I.F.S.); *Pneumodermopsis paucidens* and *Spiratella retroversa* N.W. of Cape Wrath, 1974 (D.W.McK.); *Tritonia plebeia* Port Nancon, 10.7.1975 (I.F.S.); *Chlamys striata* Papa Bank, 1974 (D.W.McK.); *Corbula gibba* N.W. of Holborn Head, 5.5.1975 (R.B.); *Thracia phaseolina* Nun Bank, 1974 (D.W.McK.); *Sepiolo atlantica* N.W. of Cape Wrath, 1974 (D.W.McK.); *Cingula alderi*, *Skenea serpuloides*, *Eulimella nitidissima* and *Astarte triangularis* were found as dead shells. An additional 19 species have been upgraded.

Orkney (3): Considerable work is now centered on Scapa Flow because of the oil industry. Records have been submitted by D. Heppell, A. Jones, D. W. McKay, Mrs. N. F. McMillan, Mrs. C. J. Pain, A. Skene jun. and I. F. Smith. *Omalogyra atomus* St. Margaret's Hope, 28.3.1975 (D.H.); *Berthella plumula* Bay of Houton, 28.3.1975 (A.J.); *Clione limacina* 59°25'N 02°25'W, 1974 (D.W.McK.); *Doto coronata* and *Eubranchius farrani* Orphir Bay, 6.7.1975 (A.S.); *Hermaea bifida* Tingwall, 8.1975 (A.S.); *Janolus cristatus* Yesnaby, 7.1975 (A.S.); *Limapontia depressa* Finstown, 24.5.1975 (I.F.S.); *Onchidoris sparsa* several

PROCEEDINGS

- localities including St. Margaret's Hope, 28.3.1975 (D.H. and I.F.S.); *Pneumodermopsis paucidens* 59°25'N 02°25'W, 1974 (D.W.McK.); *Runcina coronata* Finstown, 24.5.1975 (N.F.McM.); *Desmoteuthis megalops* 59°25'N 02°25'W, 1974 (D.W.McK.); and *Balcis monterosatoi* (dead shell) Birsay, 1972 (C.J.P.). An additional 28 species have been upgraded.
- Moray Firth (5): A detailed report for this Area has been submitted to the Conchologists' Newsletter by D. W. McKay. There are no new records but 22 species have been upgraded.
- Firth of Forth (7): *Cerithiella metula* Dunbar, 23.5.1975 Mrs. P. Nair. 5 species have been upgraded.
- Northumberland (9): F. Woodward is now Area Representative. The new list of bivalves of the Cullercoats area is nearing publication. There are no new records but 13 species have been upgraded.
- Yorkshire (11): The following are new records or new finds of species not previously confirmed, mostly recorded by C. D. Todd: *Cadlina laevis* Robin Hood's Bay, 24.7.1975 (C.D.T.); *Cuthona nana* Robin Hood's Bay, 1974 (C.D.T.); *Eubbranchus pallidus* Robin Hood's Bay, 2.1975 (C.D.T.); *Hermaea dendritica* Robin Hood's Bay, 7.1975 (C.D.T.); *Microhedyle lactea* and *Philineglossa helgolandica* offshore between Robin Hood's Bay and Whitby, 30.8.1975. 21 species have been upgraded.
- East Channel (14): *Akera bullata*, *Menestho divisa* and *Zirfaea crispata* Beachy Head, 21.9.1975, C. P. Palmer and D. Worth, dead shells only.
- Wight (15): This Area has been taken over by M. Goodchild. *Mangelia coarctata*, *Menestho dolioliformis*, *Retusa mammillata* and *Musculus niger* Poole harbour, 31.8.1975, C. P. Palmer, dead shells only.
- Portland (16): Records have been submitted by M. J. Bishop, G. H. Brown, B. E. Picton and D. R. Seaward. New records comprise: *Tonicella rubra* Ringstead Bay, 26.7.1975 (D.R.S.); *Acanthodoris pilosa* Torquay, 1974 (M.J.B.); *Coryphella lineata* Dartmouth, 8.6.1975 (B.E.P.); *Doto fragilis* Brixham, 7.6.1975 (B.E.P.); *D. pinnatifida* Portland Bill, 12.4.1975 (G.H.B.); *Embletonia pulchra* Weymouth Bay, 31.3.1975 (D.R.S.); *Eubbranchus cingulatus* Dartmouth, 7.6.1975 (B.E.P.); *E. tricolor* Brixham, 7.6.1975 (B.E.P.); *Facelina curta* Dartmouth 7.6.1975 (B.E.P.); *Janolus cristatus* Brixham, 7.6.1975 (B.E.P.); *Jorunna tomentosa* Dartmouth, 7.6.1975 (B.E.P.); *Lomanotus genei* Brixham, 7.6.1975 (B.E.P.); *Onchidoris luteocincta* Dartmouth 7.6.1975 (B.E.P.); *Polycera dubia* Ladram Bay, 1974 (M.J.B.); *P. faeroensis* Dartmouth, 7.6.1975 (B.E.P.); *Rostanga rufescens* Ladram Bay, 1974 (M.J.B.); *Trinchesia coerulea*, *T. viridis* and *Tritonia hombergii* Brixham, 7.6.1975 (B.E.P.). In addition 5 species have been upgraded.
- Plymouth (18): Most records have been submitted by B. E. Picton: *Charonia lampas* (see *J. Conch.*, Lond. **29**: 29); *Mangelia brachystoma* White Rock, 1971 (R. Manly); *Coryphella pellucida* Wembury Bay, 31.5.1975 (B.E.P.); *Facelina curta* Plymouth Sound, 31.5.1975 (B.E.P.); *Onchidoris luteocincta* Pendera Head, 23.3.1975 (B.E.P.); *Polycera faeroensis* Plymouth, 31.5.1975 (B.E.P.); and (dead shell) *Alvania lactea* Looe (M. Christie).
- Scilly Isles (19): Records of species found over a number of years have been submitted by Professor L. A. Harvey and London University Sub-aqua Club. New records include: *Ancula cristata* (L.A.H.); *Cadlina laevis*, *Dendronotus frondosus* and *Doto pinnatifida* (L.U.S.C.); *Favorinus branchialis*, *Goniodoris nodosa*, *Hermaea dendritica*, *Jorunna tomentosa*, *Limacia claviger* and *Limapontia capitata* (L.A.H.); *Polycera faeroensis* (L.U.S.C.); *Runcina coronata*, *Solecurtus chamasolen* and *Tellina squalida* (L.A.H.). Many other species have been upgraded.
- North Cornwall (20): B. E. Picton has added the following new records as a result of diving off Newquay, 28.8.1975: *Crimora papillata*, *Doto pinnatifida*, *Tritonia lineata* and *T. odhneri*.
- Cardigan Bay (22): New interest is developing in this Area. *Limapontia depressa* Mawdach Estuary, 1975, June Chatfield.
- Solway (25): Miss Milne has sent in three new records: *Heteranomia squamula*, *Nucula sulcata* and *Teredo megotara* and 9 species have been upgraded.
- Isle of Man (26): There is one new record, of a fresh dead *Pinna fragilis* dredged by a scallop boat (Larch S. Garrad), and 7 species have been upgraded.
- Belfast (28): Most recording effort has been centred on Strangford Loch, and apart from the *Sacoglossa* found by T. Gascoigne in 1974, records are the result of the survey carried out by M. Brisco and B. E. Picton in 1975. *Cingula cingillus* (M.B.); *Alderia modesta* (T.G.); *Doto pinnatifida* and *Janolus cristatus* (B.E.P.); *Limapontia depressa* (T.G.); *Lomanotus genei*, *Odostomia scalaris*, *Polycera faeroensis* (1974), *Trinchesia aurantia* and *Tritonia hombergii* (B.E.P.); *Cardium lamarcki* (M.B.); *Musculus discors* (B.E.P.). 13 species have been upgraded. *Crepidula fornicata* should be deleted.
- Minch (30): All new and upgraded records have been found offshore by D. W. McKay and Miss A. Taylor. *Clione limacina* and *Pneumodermopsis paucidens* S.E. of Tiumpán Head, 1974 (D.W.McK.); *Scaphander punctostriatus* off Barra, 1974 (A.T.); also (dead shells) *Aporrhais serresianus*, *Clathrus clathratulus* and *Lepeta caeca* off Barra, 1974 (A.T.). Two species have been upgraded.
- Lewis (31): Records for this Area are again due to the work of S. Angus and D. W. McKay. *Clione limacina*, *Pneumodermopsis paucidens* and *Spiratella retroversa* N.E. of North Rona, 1974 (D.W.McK.); *Cardium minimum* N. of Butt of Lewis, 1974 (D.W.McK.); *Chlamys similis* N.W. of Sulisker, 1974 (D.W.McK.); *Scrobicularia plana* Crowlista, 8.1975 (S.A.). Three species have been upgraded.
- Uist (32): S. Angus and D. W. McKay have submitted the following new records: *Clione limacina*, *Pneumo-*

dermopsis paucidens and *Spiratella retroversa* S. of St. Kilda, 1974 (D.W.McK.); *Philine aperta* Loch Leosavay, 1975 (S.A.); *Leucophytia bidentata* and *Anomia ephippium* South Harris, 1974 (S.A.); *Cultellus pellucidus* and *Thyasira flexuosa* (dead shell) Loch Leosavay, 1975 (S.A.).

Galway Bay (36): The following new records have been found by D. McGrath diving in Galway Bay, 1975: *Acanthochitona communis*, *Lepidopleurus cancellatus*, *Natica fusca*, *Paludinella littorina*, *Philine scabra*, *Roxania utriculus*. *Parastrophia folini* should be deleted.

Fastnet (37): L. Atkins reports that 5 specimens of *Galeodea rugosa* were trawled 27 miles west of Sybil Point in 1968.

S. M. SMITH

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GOULD, S. J. 1969. An evolutionary microcosm: Pleistocene and Recent history of the land snail *P. (Poecilozonites)* in Bermuda. *Bull. Mus. comp. Zool. Harv.* **138**: 407–532, 5 pls.

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Mollusks

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Overseas members are reminded that all monies due to the Society are payable in sterling.

SOME REMARKS ON *ACICULA* S.S. (PROSOBRANCHIA: RISSOACEA)

E. GITTENBERGER

Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands

AND

H. D. BOETERS

Rumfordstrasse 42, D 8 München, West Germany

(Read before the Society, 2 October 1976)

Abstract: An attempt to identify an *Acicula* from Gibraltar not only lead to the conclusion that it was an undescribed species, but also to the discovery that *A. (A.) lallemanti* (Bourguignat) from Algeria included two distinct species. *A. (A.) lallemanti* is restricted by definition of a lectotype and is described together with *A. (A.) algerensis* nov. and *A. (A.) norrisi* nov. from Gibraltar. All three species are figured with *A. (A.) lineata* and *A. (A.) sublineata* for comparison.

The species recognized as belonging to the graceful operculate terrestrial snail subgenus *Acicula* s.str., known to occur with large distributional gaps in the western palaearctic region, are characterized by glossy, nearly cylindrical small shells, ornamented by sharp, radially engraved lines. Ehrmann (1908), Kobelt (1908) and Hesse (1920) gave reviews of all taxa known to them. There is no recent monograph in which the subgenus is dealt with and, as many descriptions are inaccurate, much confusion occurs and our systematic and zoogeographical knowledge concerning the group is still very incomplete. Nevertheless, seven shells belonging to *Acicula* s.str., collected at Gibraltar by Mr. A. Norris, show a combination of characters so clearly different from those known to occur in the other taxa within the subgenus that the description of a new species seems justifiable. A single specimen of most probably the same species, also collected at Gibraltar, is mentioned as *Acme* n. sp. by Ponsonby (1885, p. 266) and as *Pupula* spec. nov. by Hesse (1920, p. 88). So the species was discovered nearly a century ago, but it has remained undescribed until now.

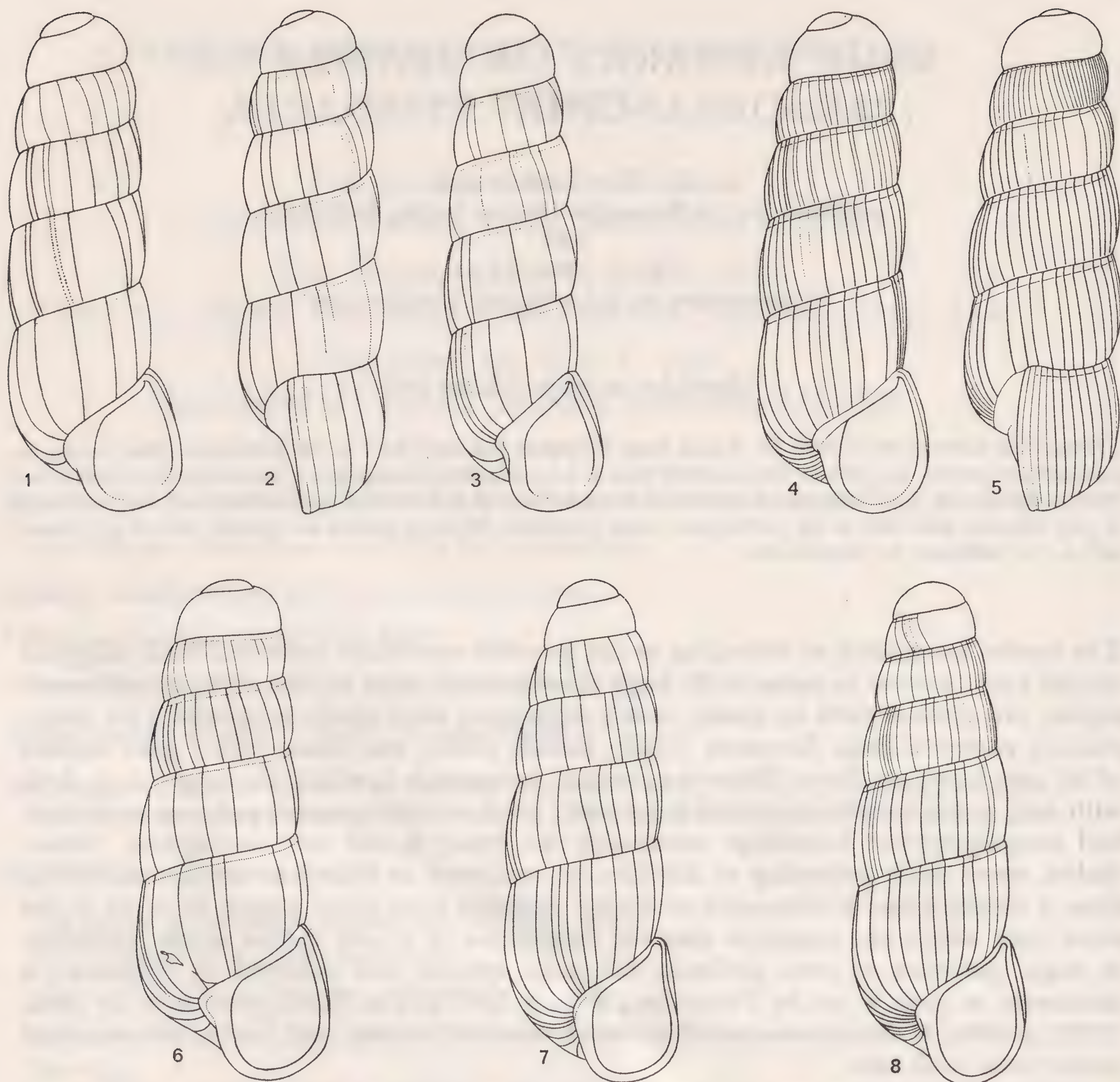
While studying syntypes of the Algerian *Acme lallemanti* Bourguignat, 1864, for a comparison with the Gibraltar form, an astonishing discovery was made. The syntypes could easily be divided into two groups, showing specific differences. Bourguignat, well known master of splitting, was a lumpner in this case. Both species from Algeria are clearly different from the European members of the subgenus. Hence, the name *A. lallemanti* is fixed by designation of a lectotype and a new name is given to the second Algerian species.

A. (A.) lineata (Draparnaud 1801) and *A. (A.) sublineata* (Andreae 1883) are provisionally interpreted in the present paper in conformity with Ehrmann (1933, p. 182-183, pl. 8, figs. 111-112).

The shells figured in this paper are shown at different magnifications, thus enabling an easy comparison of the morphology of the various forms.

Abbreviations used: BM = British Museum (Natural History); MHNG = Muséum d'Histoire Naturelle, Genève; RMNH = Rijksmuseum van Natuurlijke Historie, Leiden.

We are indebted to Dr. E. Binder (Geneva) who allowed us to study the Bourguignat material, and especially to Mr. A. Norris (Leeds) who sent us the interesting Gibraltar *Acicula*, having already noted its peculiarity.



Figs. 1–3. *Acicula (Acicula) norrisi* spec. nov., Gibraltar, A. Norris leg. 1–15. IV. 1975. 1–2, holotype, actual height 3.1 mm (BM 1975640). 3, paratype, actual height 3.5 mm (Norris collection).

Figs. 4–5. *Acicula (Acicula) lallemanti* (Bourguignat), near Algiers (see text), lectotype, actual height 3.1 mm (MHNG).

Fig. 6. *Acicula (Acicula) algerensis* spec. nov., near Algiers (see text), holotype, actual height 3.4 mm (MHNG).

Fig. 7. *Acicula (Acicula) sublineata* (Andreae), Italy, Bérghamo, Bracca, Costa di Serina, 500 m alt., E. Gittenberger leg. 6. IX. 1974, actual height 3.0 mm (RMNH).

Fig. 8. *Acicula (Acicula) lineata* (Draparnaud) (subsp. ?), Italy, Bérghamo, Bracca, Costa di Serina, 500 m alt., E. Gittenberger leg. 6. IX. 1974, actual height 3.6 mm (RMNH).

DESCRIPTIONS

Acicula (Acicula) norrisi sp. nov. (Figs. 1–3)

The light-brown shell has a relatively broad apex, a narrow spire and 6–6½ whorls, increasing regularly but extremely slowly in breadth. The palatal border of the aperture diverges conspicuously from the shell-axis (in front view), it passes rather abruptly into the oblique, slightly bent basal border. So the character of the aperture disturbs the general cylindriform shell outline to a relatively great extent and, moreover, increases

the total breadth of the shell quite considerably. An upper palatal sinus is not developed. The umbilicus is closed by a callus which is bordered by a marked ridge. The engraved radial lines are generally widely spaced: 15–20 on the last whorl.

Measurements: height 3.1–3.5 mm; breadth 1.1–1.5 mm.

A. (A.) norrisi has a shell which is more closely cylindriform and narrower than usual in *Acicula* s.str. The radial lines are widely spaced as for example in *A. (A.) beneckeii* (Andreae 1883, p. 137, fig. 1) (see also Gittenberger and Ripken 1975, p. 12, fig. 2) and *A. (A.) algerensis* spec. nov. (Fig. 6), both differing by a clearly less cylindrical shell and larger dimensions. Additionally *A. (A.) beneckeii* has an upper palatal sinus and *A. (A.) algerensis* possesses a broader umbilical callus, separated only by a weakly developed ridge from the body-whorl. *A. (A.) lallemanti* and *A. (A.) algerensis* both have a broad apex like *A. (A.) norrisi* and in contrast to *A. (A.) beneckeii*, *A. (A.) lineata* (Fig. 8) and *A. (A.) sublineata* (Fig. 7). *A. (A.) lallemanti* can be separated from *A. (A.) norrisi* by the more numerous radial lines and a different form of the aperture, *A. (A.) algerensis* has already been differentiated before. Also among the other taxa of *Acicula* s.s., known to us mainly from literature, there seems to be no species coming particularly near to *A. (A.) norrisi*. A working hypothesis may be that it belongs to a southern species group, characterized by relatively broad apices.

All specimens were collected by Mr. A. Norris at Gibraltar (locus typicus), 1–15 April 1975. The geographically nearest species are *A. (A.) algerensis* and *A. (A.) lallemanti*, both known from Algeria and *A. (A.) pyrenaica* (De Folin and Bérillon 1877), which is found in the Pyrenees.

Derivatio nominis: after Mr. A. Norris.

Material. – Holotype: BM 1975640. Paratypes: City Museum collections, Leeds (1 specimen); Norris collection (4 specimens, among which one figured); RMNH (1 specimen, Nr. 55117).

Acicula (Acicula) algerensis sp. nov. (Fig. 6)

The colourless shell has a relatively broad apex and $5\frac{1}{2}$ –6 whorls, increasing slowly and regularly in breadth. The aperture does not show any peculiarities. An upper palatal sinus is lacking. The umbilicus is closed by a broad callus, which is separated by an inconspicuous ridge from the body-whorl. The engraved radial lines are rather widely spaced: 20–26 on the last whorl.

Measurements: height 3.25–3.4 mm; breadth 1.1–1.3 mm.

A. (A.) algerensis differs from the sympatric *A. (A.) lallemanti* most clearly by being larger, less cylindrical, less densely striated and colourless. The last mentioned character has to be confirmed, as the few shells known might have faded. See further the remarks under *A. (A.) norrisi*.

All specimens of *A. (A.) algerensis* known belong to the former syntypes of *A. (A.) lallemanti*.

Derivatio nominis: living in Algeria.

Material. – Holotype: MHNG, labelled 'alluv. du frais-vallon et Chabet-Beinan près Alger' (after Bourguignat, 1864, p. 221: 'Alluvions à l'écluse du Frais-Vallon près d'Alger' and 'à Chabet-Beinan, entre Alger et Sidi-Ferruch'). Paratypes (all in MHNG): locus typicus (an apical fragment of about 3 whorls, a juvenile shell of 5 whorls); labelled 'Maison Carrée près Alger' (after Bourguignat, 1864, p. 221: 'alluvions de l'Harrach près de la Maison-Carrée') (2 specimens, adult).

Acicula (Acicula) lallemanti (Bourguignat, 1864) (Figs. 4–5)

The light-brown shell has a relatively broad apex and about 6 whorls, increasing regularly but very slowly in breadth. The aperture does not show any peculiarities. An upper palatal sinus is lacking. The umbilicus is wholly or partly covered by a rather narrow callus, which is separated from the last whorl by a clear ridge. The engraved radial lines are narrowly spaced: 26–33 on the last whorl (21 in a specimen which is normal in all other characters).

Measurements: height 3.0–3.3 mm; breadth 1.0–1.1 mm.

See further the remarks under the preceding species.

Material. – Lectotype: MHNG, labelled 'alluv. du frais-vallon et Chabet-Beinan près Alger' (after Bourguignat, 1864, p. 221: 'Alluvions à l'écluse du Frais-Vallon près d'Alger' and 'à Chabet-Beinan, entre Alger et Sidi-Ferruch') (Figs. 4–5). Paralectotypes (all in MHNG): locus typicus (14 specimens); labelled 'cascade de la glacière près Blidah' (after Bourguignat, 1864, p. 221: 'cascade de la Glacière . . . près de Blidah') (3 specimens).

The following samples originate from localities not mentioned by Bourguignat (1864), but present in his collection and labelled '*Acme lallemanti*' there: 'alluv. du Safsaf près Philippeville' (1 specimen); 'detritus de la Macta, près d'Oran' (1 specimen); 'Cap Caxine près Alger' (3 specimens); 'Tizir'ir, au dessus des gorges de l'Oued Isser (Kabylie)' (1 specimen).

No material was seen from the localities 'Aïn-Tlezid près de Blidah' and 'alluvions de la Boudjimah, près de Bône', both mentioned by Bourguignat (1864, p. 221).

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THE UNIQUENESS OF THE POLYMORPHISM OF *CEPAEA* (PULMONATA: HELICIDAE) IN WESTERN EUROPE

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Abstract: The polymorphism of shell colour and banding in *Cepaea nemoralis* is the most vivid of any species of land snail in western Europe. Rules of colour variation in relation to degree of exposure to sunlight have been suggested by Pilsbry for North American snails in particular, with an indication that they are of general validity. A survey of shell colour and banding in west European snails in relation to habits and habitat using data from Germain confirms Pilsbry's generalizations for whiteness and opacity in very exposed species, and dull brown colour and transparency in very secretive species or those in shady habitats. Certainly at the extreme of shading and probably at that of exposure, no polymorphism is normally visible; highly polymorphic species including *C. nemoralis* have intermediate habits, and occur in a considerable variety of vegetation, being often visible during the day but not exposed for weeks on end to extreme insolation. The polymorphism in *Cepaea nemoralis* is a marked example of a more general phenomenon, probably appropriate to its mode of life.

At first sight the extraordinarily bright colours and the contrasting dark banding of the shell of *Cepaea*, especially of *C. nemoralis*, seem unique among the land snails of western Europe, the more so when the great diversity of individuals within most populations is also taken into account. Although there is still much room for speculation on the maintenance of the polymorphism and the principal factors affecting it, it is generally agreed that the polymorphism is heavily influenced by natural selection (see Williamson 1972 for a brief account). But if selection is acting, it is likely that the polymorphism bears some relation to the ecological characteristics of the genus. Direct analysis by ecogenetical methods is often extremely difficult; this paper approaches the problem by a survey of the variation and ecology of the land-snail fauna of western Europe.

The nomenclature used for the North American fauna is that in Pilsbry (1939-1948). For the west European fauna Waldén's (1976) is used, as it is the latest list, but where necessary Germain's (1930) is given in parentheses to avoid confusion.

COLOUR VARIATION AND EXPOSURE IN HELICACEA

It has often been remarked that snails exposed to strong insolation tend to have white opaque shells. For example, Pilsbry (1939, p. 415), discussing the genus *Oreohelix* (Camaenidae Oreohelicinae in his classification; a separate family in Taylor and Sohl, 1962) remarks 'The opaque, whitish and earthy texture of *Oreohelix* shells of the semiarid states is a protective adaptation to the strong light of a high country with little shade. It is a character common to snails exposed to strong insolation all over the world.' He notes, with respect to *Oreohelix clappi* and *O. barbata*, that they 'live only where deep rock slides in shaded ravines afford constant humid conditions. These shells have colour and texture like snails of moist regions. *O. subrudis*, which has a chalky white shell in dry regions, is thin and dark coloured in the aspen zone of the Black Range, N. M., living

on densely wooded slopes where the forest humus is deep and moist.' He notices similar variation in the Helminthoglyptidae Helminthoglyptinae where they produce desert species (1939, p. 159 on, compare with the Californian coastal species). In a very different family (Polygyridae Polygyrinae) he notes (1940, p. 689) of the genus *Praticolella*, 'The shells are either pale cinnamon or translucent grayish, uniform or with a brown band above periphery, or they are opaque white, uniform or with brownish or translucent-gray bands. Those of uniform brownish colour are partly ground snails, but others, together with the white and white-banded forms ascend grass or bushes.' In both their habits and their colours these latter are in striking contrast to the other species of the genus and to the rest of the eastern American Polygyridae which are almost all secretive, nocturnal, ground-living, and nearly uniformly some shade of brown.

The parallels with the west European fauna are obvious. Within the Helicidae, *Theba* (= *Euparypha*), *Marmorana*, and some others of the Helicinae sit out in full sun as do almost all *Helicella* (Helicellinae), while such dully-coloured forms as *Helix aspersa* (Helicinae) are normally far more nocturnal, although they may emerge on very dull wet days. Similarly in the Enidae, *Ena* is very much a forest, thicket and hedge form and is brown, while *Zebrina detrita* is nearly white and lives conspicuously exposed to full sun.

Within the European Helicidae there is a good deal of variation in habits and habitat, seldom adequately documented. For this paper, I use the observations made by an independent witness, Germain, in his first volume in the *Faune de France* (1930), which contains virtually all the British species as well, and class each species in the Helicacea according to his notes, as dark-coloured, medium, light with darker bands or maculations, and white; and according to their habits and habitats as

- (a) nocturnal and buried during the day, or in very shady habitats,
- (b) more or less nocturnal, burying at least during summer heat, or in definitely shady habitats,
- (c) of general habitat-distribution, sometimes exposed, sitting out on rocks or vegetation,
- (d) in exposed habitats, and
- (e) in very exposed habitats (extreme xerophile) and sitting out.

From these we obtain Table 1. Since in Britain *Cepaea nemoralis* is usually yellow, pink or dark brown, and unbanded, midbanded or five-banded, i.e. both light and dark, it has been scored as 'medium', and *C. hortensis* likewise since it is usually yellow unbanded or yellow five-banded, the latter often being quite dark. In European populations where *nemoralis* is largely yellow and few-banded, it could well be classed as light with bands, as could *hortensis* (or *vindobonensis*), but the result would hardly be altered. To obtain expectations of more than 5 the top two lines are combined, as are the bottom two, and columns (b) and (c). The result is highly significant (P much less than 0.001). Inspection of the table shows that the lighter-coloured shells are heavily associated with exposed habitats, the darker ones with shady habitats and/or nocturnal habits, even on this crude scoring.

Germain's comments on the transparency, or subtransparency, or thinness with fragility (and hence likely transparency) of the shell in some species, and of its opaqueness in others also agree with Pilsbry's comment on the opacity of species that sit out in the sun. Fairly or markedly transparent shells are found in 15 out of the 42 species in columns (a), (b) and (c) combined, with the highest proportion in column (a). In column (d) and (e), the definitely exposed species, there are only 4 in 15 in (d), none in 20 in (e). A χ^2 test with the intermediate column (c) combined with (a) and (b) gives P between 0.02 and 0.01; if it is combined with (d) and (e), P is between 0.01 and 0.001. There is a definite indication, therefore, that more transparent shells are associated with more

shady habitats and/or more secretive habits.

It is interesting that in *Helicella itala* (= *ericetorum*) shells with transparent bands (unpigmented), or only partly pigmented ones, and others with the shell opaque only in certain parts (blotchy), were found in some abundance as a definite polymorphism in north-west Scotland, where the number of rain-days is high and the insolation poor (Cain, Cameron and Parkin 1969). I have since found a colony with a high proportion of hyalozonate bands in north-west Ireland under rather similar conditions. Also, Parkin (1972) has found the albino form of *Arianta arbustorum*, the so-called yellow, to occur mainly in regions of high rainfall. It is possible that the hyalozonate form of *C. nemoralis* may show a similar distribution overall. When much more is known of the geographical distribution of the frequency of morphs, not their bare occurrence, this tendency towards comparative transparency of shell where insolation is reduced may be found in several species. As darker shells can also be tolerated under such conditions or may be selected for (Cain, Cameron and Parkin 1969), a polymorphism may be allowed.

The four species that are noted by Germain as more or less transparent-shelled and as in exposed habitats are *Trichia* (= *Monacha*) *glabella* and *Monacha* (= *Theba*) *cantiana*, *cartusiana*, and *cemenelea*; all are recorded from bushy areas as well, and perhaps may really belong to column (c), but *Monacha cantiana* (= *Theba cantiana*) certainly sits out well exposed in the oceanic climate of Britain.

TABLE 1

Association between shell colour and habitat or habits

	(a)	(b)	(c)	(d)	(e)	TOTALS
dark	9	5	—	—	—	14
medium	8	10	7	4	—	29
light	—	1	2	10	17	30
white	—	—	—	1	3	4
TOTALS	17	16	9	15	20	77

Combining dark and medium shells, and light and white, and columns (b) and (c), to obtain adequate expectancies, $\chi^2_3 = 54.4$, $P < 0.001$. Data from Germain, *Faune de France* (excluding introduced forms, synonyms, forms not in France, and a few for which adequate data are not given) for Helicidae and Bradybaenidae (= Eulotidae; only *Bradybaena fruticum* in France).

POLYMORPHISM AND EXPOSURE IN HELICACEA

If each species in Table 1 is scored for uniformity or definite polymorphism of shell colour and ornament, we find that none are polymorphic in the first two columns, a total of 0 in 33; 8 out of 9 are, in column (c), 10 out of 15 in (d) and 14 out of 20 in (e). A χ^2_1 test gives P much less than 0.001, even if column (c) is combined with (a) and (b). Clearly, uniformity of colour is very closely associated with the woodland habitat and/or with secretive habits, while even moderate exposure, as in column (c) species, is associated with polymorphism at least of banding. Interestingly, in columns (d) and (e) are a few species which are either always white, white but rarely banded, or (*Helicella* (*Jacosta*) *explanata*) white with a very pale band on the upper surface, and these species are among those marked as most xerophile of all. The data are too scanty to reach a firm conclusion, but it appears that extremely exposed species become effectively monomorphic again. Certainly elsewhere, such species as *Levantina hierosolyma* and *L. caesareana*, that occur on arid rocks in Israel, are monomorphic, white with faint brownish marblings, and Dr. J. Heller (to whom I owe my specimens) tells me that *Theba* (= *Euparypha*) *pisana* in the hottest part of its range in Israel becomes plain white. Of the other species in columns

(d) and (e), almost all show a polymorphism in banding only, except that both a plain white and a pale ginger shell colour occur in several species of *Helicella*. In *Cochlicella acuta* (column (e)), a flecked ginger form is common and very cryptic on sand in Britain, but Lewis (1968, 1975) who discovered this association, noted that in the south of this species' range in western Europe, plain white shells became predominant. There is, then, a clear tendency to monomorphic brown shells in columns (a) and (b), and a probable one to effectively monomorphic white or nearly white shells in species exposed to very hot sun, affecting some species in column (e).

Of the species in columns (a) and (b), only *Arianta arbustorum*, *Helix aspersa*, and perhaps *Trichia hispida* are at all polymorphic. The accounts and illustrations given in Germain (1930), Taylor (1894–1921) and similar monographs aim at complete description and usually greatly exaggerate the amount of variation to be expected within a population. Thus *Helicella itala* (= *ericetorum*) with 14 varieties of banding alone in Taylor, has in most of England a shell with, on the exposed part, a ground colour of (slightly brownish) white with a single dark band; it is in regions with a large number of rain-days, such as north-west Scotland, as mentioned above, that considerable variation is to be found on the upper parts of the shell (Cain, Cameron and Parkin 1969). The commonest form of *Helix aspersa* in Britain has the band-formula 1(23)45. Individual shells with various degrees of further fusion of the bands are found, not infrequently reaching (12345), but the variation appears to be continuous. On dark backgrounds, shells with wider and more fused bands are commoner, but in most populations I have seen in Britain there is no polymorphism. The polymorphism in shell colour which I described (Cain 1971) is only from a reddish brown to a yellow brown, clear enough in bred material but often hardly scorable in more than a few adult shells in random samples. Similarly, in *Arianta arbustorum* there is a considerable range in shell colour from nearly black-brown (reddish) to pale yellow, but seldom anything that can be scored as a polymorphism in random samples. An albino form, yellow only because of the periostracum, occurs in some populations (as it does rarely in *H. aspersa*), and Parkin (1972) has shown that in Britain it appears in any frequency only in high-rainfall areas. *Trichia hispida* usually has a dark red-brown shell, but pale brown ones occur as a definite polymorphism.

The species in column (c) are *Cepaea sylvatica*, *C. nemoralis*, and *C. hortensis*, *Helix pomatia*, *Euomphalia strigella*, *Trichia* (= *Fruticicola*) *striolata*, and the only west European bradybaenid, *Bradybaena* (= *Eulota*) *fruticum*, all classed as with medium colour; and *Eobania vermiculata* and *Helicella conspurcata* with light shells. Of these, *H. pomatia* has a muted-down polymorphism in rather pale brown banding only, and tends to be paler than *H. aspersa*; the shell is very thick, and what little experience I have of the species in England and France suggests that it may expose itself to light much more than *H. aspersa*. *T. striolata* has a polymorphism involving both shell and body colour (Cain 1959a, b), the two being linked, so that a dark red shell and dark body often go together, and a paler, fawn-brown shell with light body-colour. *T. striolata* is often abundant in rough herbage by the side of roads, and other open habitats, and not infrequently exposed to light, more so in my experience than *T. hispida*. *Euomphalia strigella* according to Germain lives in a variety of habitats but avoids those strongly shaded or very humid; the shell is pale horn, fulvous, or reddish, with or without a milky zone along the periphery (also seen in *T. striolata*). This species appears to be a submontane replacement for *T. striolata*, and should be investigated for polymorphism. *Helicella conspurcata* is almost the only helicelline that is often found in association with bushes and trees as well as in open habitats; it has a reddish or horn-tinged grey shell with brown mottlings. It may perhaps belong to column (d), but, there being a doubt, it is included in column (c) as thereby acting against the hypothesis of association of colour and habitat being tested. *Eobania vermiculata* is placed here for the same reason.

The remaining species in column (c) are much more conspicuously polymorphic. *Bradybaena fruticum* has a white, yellow, or horn-brown shell, with or without a dark median band and occupies much the same range of habitats, and shows the same habits (Germain 1930, p. 173) as *Cepaea nemoralis* or *hortensis*; it lacks a five-banded morph. *C. sylvatica*, a montane form, is nearly monomorphic yellow-white five-banded. *C. hortensis* and *C. nemoralis* have the same polymorphism (Taylor, pls. 26, 28), with shades of yellow, red and brown, and unbanded, single-banded, and variously-modified five-banded morphs. The species of columns (d) and (e) show nothing like this colour-range, and even those that have an extraordinary degree of variation of bands on the underside of the shell are often unvarying above, with a white or pale brownish white shell and a dark band. Several species, e.g. *Cernuella virgata* (= *Helicella variabilis*) have a vinous or purplish tinge around the mouth of the adult shell (and I have found in western Ireland, a polymorphism in *H. ericetorum* (= *itala*) with one morph wholly claret-coloured). Only *Pseudotachea splendida*, with yellowish-white shell, unbanded or more usually five-banded with bands 1, 2, 3 and 5 usually broken into spots, approaches any of the species in column (c).

In *Cepaea* the shell is often translucent enough for the colour of the body to show through, and modify the shell colours. Thus a bright yellow shell in *C. nemoralis* with a nearly black body inside is effectively grass green. In *Monacha cantiana* the shell is not polymorphic but the body in southern English colonies often is, and a dark and a light morph are found, seen by transparency through the shell (Cain 1971). Strictly, therefore, an investigation is needed into the *effective* colour of the live animals, not that of the empty shell. It is certainly true in England that many species of woodland snail have dark bodies, reinforcing the dark shell colour.

Even on the crude scores obtainable from Germain's data (not compiled for this purpose), which are in agreement with my experience in Britain and France, a really rich polymorphism is associated with habits of not infrequent exposure and with occurrence on a great variety of backgrounds. Very nocturnal and/or woodland forms are uniformly brownish; those that are normally exposed to strong sun have an opaque shell with a white shell-colour or nearly so, decorated with dark bands, and those extremely exposed may tend towards a white monomorphism. As far as *Cepaea* has a parallel, it is found in shell colour in the bradybaenid *Bradybaena fruticum*, on the same variety of backgrounds, and in banding in the helicines *Otala* (= *Archelix*), *Marmorana*, *Pseudotachea*, in a few of the less extremely exposed Helicellines, and (muted down) in the more nocturnal *Helix aspersa*.

OTHER SNAIL SUPERFAMILIES

Among the rest of the land stylommatophora of western Europe with well-developed shells, the majority of shells are brown, with little variation (except for rare and sporadic albinos, which may occur in any species without constituting a polymorphism, or only a very restricted one geographically). Almost all these forms are either woodland dwellers, or secretive even when living in short vegetation in exposed positions. This is true of the west European Zonitidae, Endodontidae, Stenogyridae, Cochlicopidae (= Cionellidae), and most Clausiliidae, Enidae except *Zebrina*, Chondrinidae, Orculidae and Pupillidae. (Minute forms (Vertiginidae, Valloniidae) are not considered here, but the same is probably true for them). These, therefore are mainly species for columns (a) and (b) in the table, and *Zebrina detrita* for column (d) or more probably (e). Even some of the rock-haunting Clausiliids will vanish into clefts and fissures in the presence of bright sunlight, and hide themselves. While it is desirable, therefore, to obtain much more precise data on the European species, it appears that the regularities alluded to by

Pilsbry, who had vast experience of the world's terrestrial gastropods, hold as well for the European stylommatophora generally as for the Californian helminthoglyptids and eastern American polygyrids. They can be expected to hold equally well for terrestrial operculates (Cain, in preparation).

DISCUSSION

There seems no reason to doubt that the brownness of so many nocturnal and woodland leaf-litter species is cryptic. As a matter of field experience, the English ones are hard to see at night even with a torch (unless actually moving) while dead whitened shells stand out conspicuously. By day, most are concealed and must be searched for. By contrast, the white and black-banded shells that sit out on herbage are not inconspicuous at night, and are obvious during the day. They contrast far more with vegetation, even if dead and dried, than do many varieties of *Cepaea* on richly coloured and diverse backgrounds. It is true that the colour patterns of *Cepaea* are not as protective as those of some well-known moths, that sit upon lichenized tree-trunks and are almost imperceptible. In a locality where *nemoralis* is common it is usually easy to find a few quickly; only when one gets down on hands and knees and searches, does one find how many and of what colours and patterns have been missed. This is an important point. Mathematical population geneticists (Sir R. A. Fisher, J. B. S. Haldane, Sewall Wright) agree that even 1% selection is from an evolutionary point of view strong enough to determine the frequency of an allele against mutation pressure and most random processes except in extremely small populations (see e.g. Falconer 1960). If of two variants, therefore, one is overlooked on average once for every ninety nine times it is seen by predators, while the other is not, the more cryptic one will spread at the expense of the other to fixation or to some equilibrium frequency if balanced polymorphism is involved. To observe such a differential in the wild is in general impossible since enormous samples would be required, and populations are not usually dense enough. To observe it in our own collecting is equally impossible without careful investigation. It follows that because various black and white banded shells seem equally conspicuous to us, we are not entitled to conclude that they are exactly equivalent to us and to predators, and that no element of crypsis is present.

It has been known ever since Benjamin Franklin's classic experiments in the 18th century, that dark materials absorb and convert to heat far more solar radiation than do light ones. A white shell is therefore better adapted to reflect radiation and remain comparatively cool in highly insolated regions, and if protection from heat overrides all other considerations, the shell should only be white, at least on the habitually exposed parts. Slight pale mottling may be tolerated in such forms as *Levantina* as partial crypsis on white limestone rock of irregular texture or mottled colour. In most species of *Helicella*, and common morphs of *Eobania vermiculata*, *Otala lactea* and *Iberus (Massylaea) marmoratus* which I have observed in Gibraltar, the flecks of the mottling and the bands may be very dark. Presumably a black spot or band on a thick opaque shell will convert radiation to heat as it arrives on the outer surface, and it can then be dissipated by conduction to the adjacent air and subsequent convection. Mottling, again, may be cryptic; but why should black bands appear at all on the upper surface of the shell? It is useless to refer to ancestral characters, pleiotropic effects, coadapted genotypes, and other attempts not to explain these characters but to explain them away. In most of these species an un-banded morph is known or even frequent, and the banded form must be maintained against it by selection. Since in *Cochlicella*, at least, more-banded forms are dominant to less-banded (Lewis, 1975) banding is not a recessive character merely appearing when it cannot be suppressed. If really cryptic patterns would involve colours too absorptive to be tolerated in exposed conditions, as when *Helicella virgata* should be rich green on

green grass, then at least a disruptive pattern in black and white may be better than a totally conspicuous whiteness. Lewis (1968, 1975) has noted this for *Cochlicella acuta*. Even in *Cepaea nemoralis*, Cain and Sheppard (1954) found that the disfavoured colour morph (yellow) in woodlands was more banded than the favoured (pink) and suggested that this was improved camouflage by breaking up the more conspicuous colour. Clarke (1960) has applied the same principle to variation in *C. hortensis* with success.

Both *Cepaea* and *Bradybaena fruticum* are often found in rather more humid habitats than many species of *Helicella*, certainly more than *Leucochroa candidissima*, *Theba pisana*, or *Helicella explanata*. More humid habitats either experience more rain-days and less sun, or tend to have more lush vegetation, with consequent shading, than do arid ones. Sitting out in more open habitats, as these species often do, they are visible against varied backgrounds, unlike snails of dense woodland leaf-litter. Moreover, *Cepaea* is a quite large snail; for the shell to blend in with a given natural background, in which the individual elements of colour, light and shade may be quite small, the shell will often need to be broken up, either cryptically or disruptively or both. It would seem, therefore, that the remarkable polymorphism in *Cepaea* is appropriate to its habits and normal habitats. The questions to be asked are why *C. sylvatica* is nearly monomorphic, why *B. fruticum* does not need a five-banded morph, what snails in other continents have the same sort of habitats and habits, and what their variation is.

In this connection, *Balea perversa* is instructive. Although hardly ever on the ground and perhaps the nearest British approach to a tree (and rock) snail (Boycott 1929, 1934), it is not highly polymorphic in colour and pattern, being brown with pale striations. Other tree snails, such as *Liguus* in Florida and the Caribbean, and indeed those winkles that have become tree snails on mangroves (see e.g. Rosewater, 1970) are sometimes brightly coloured. But *Balea* is a small snail, apt to hide away in crevices in tree trunks, and indeed not found on smooth trunks. Only when snails are to be seen against a highly diversified background (leaves, branches, flowers, fruit, and sky) will they be brightly coloured, and only if large disrupted by obvious bands or patches. A nocturnal tree snail, found only in crevices in bark during the day can well be monomorphic brown, and one entirely on leaves monomorphic green.

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HELICODISCUS SINGLEYANUS (PILSBRY) (PULMONATA: ENDODONTIDAE) FOUND IN THE BRITISH ISLES

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Abstract: *Helicodiscus singleyanus* (Pilsbry), a small land snail known from North America and, more recently, from scattered sites in Europe, is now recorded from the British Isles. Three shells were found at St. Ouen, Jersey, one at Machynlleth, Dyfed, one in Kew Gardens, Surrey and two at Whipsnade, Bedfordshire. Of the European snails found in leaf litter, *H. singleyanus* most resembles *Vitrea* spp., from the shells of which it is distinguished by the large open umbilicus.

Helicodiscus singleyanus (Pilsbry) is a North American land snail belonging to the family Endodontidae. In the United States it occurs from New Jersey south to Florida on the Atlantic coast, and west to Arizona (Pilsbry 1948). Its distribution falls in the latitude range 30-45°N. There is also a record of its introduction into a garden in California where living specimens were seen (Pilsbry 1948). The sub-species *H. singleyanus inermis* Baker occurs in the same general geographical range in the U.S.A. *Helicodiscus singleyanus* is not on the list of land snails for Canada (La Rocque 1953).

In addition to North America, a number of distribution records have been published for this snail in Europe during the last thirty years. These include the Netherlands (Kuiper 1949, 1956; Gittenberger, Backhuys and Ripken 1970; Schmid 1970), Belgium (Gittenberger, Backhuys and Ripken 1970), Germany (Kadolsky 1967; Schmid 1969), France (Altena 1961), Switzerland (Kuiper 1949, 1956), Austria (Kuiper 1956; Altena 1961) and Spain (Gittenberger, Backhuys and Ripken 1970). There is a fossil record (one shell only) from the Pleistocene in Czechoslovakia (Lozek 1964). In Europe this snail seems to occupy a more northern distribution in a latitude range of about 40-50°N.

HELICODISCUS SINGLEYANUS IN THE BRITISH ISLES

In 1975 *Helicodiscus singleyanus* was identified from two localities in the British Isles and two further records were made in 1976. The first of these finds consisted of three shells from La Bergerie, St. Ouen, Jersey (U.T.M. grid reference WV 555556). The shells were found in a soil sample taken from a depth of about 60 cms during an archaeological excavation in October 1974. The soil was neutral with a pH of 7. The shells were found by Mrs. Mary Siddaway and Dr. John Renouf during the examination of soil samples from the site, and they were sent to the author for identification. These specimens were thin but the periostracum (outer horny layer of the shell) was still present, which suggested that they were not sub-fossil; but there was no trace of an animal within them.

The second discovery was from Ynys-hir Hall on the south of the Dovey estuary near Machynlleth, Dyfed (National Grid reference 22/682958). This came from a bag of mixed leaf litter collected from a wood by Mr. and Mrs. C. G. Trew in September 1975. The leaf litter was dried and sorted for land molluscs. One shell of *H. singleyanus* was present together with *Carychium minimum* Müller, *Punctum pygmaeum* (Draparnaud), *Discus*

rotundatus (Müller), *Oxychilus alliarius* (Miller), *Nesovitrea hammonis* (Ström), *Zonitoides excavatus* (Alder) and *Vitrina pellucida* (Müller): these are all snails typical of damp litter.

The third and fourth records of *Helicodiscus singleyanus* in Britain were made by Dr. A. Rundle in 1976 and subsequently verified by Dr. M. P. Kerney. Two shells were found under pieces of wood near a brick wall in the yard of Dell Farm Field Centre, Whipsnade, Bedfordshire (52/005180) in May 1976 and in June 1976 one shell was found in friable soil under mixed deciduous leaf litter near a wall, south-east of the refreshment pavilion in Kew Gardens, Surrey (51/187761).

Some of the specimens from Jersey are likely to be housed in a museum on the mainland (probably Cardiff) but this is still under discussion. The shell from Machynlleth and the associated molluscan fauna is in the National Museum of Wales, Cardiff (N.M.W. Accession number 76.68.Z) and those from Kew Gardens and Whipsnade in the collection of Dr. A. J. Rundle.

DIAGNOSTIC CHARACTERS

The first specimens of *Helicodiscus* from Jersey were whitish in colour, thin-shelled, smooth, shiny, somewhat translucent and, being tightly coiled, they resembled *Vitrea* spp. in size and in appearance in dorsal view. However when a shell was turned over, there was a large open umbilicus more like that of *Vallonia* spp. or *Discus rotundatus* than *Vitrea*. As few members of the Society are likely to have access to a copy of Pilsbry (1948) a brief description is given to help conchologists recognize future findings of this snail.

The shell of *H. singleyanus* is figured in Kuiper (1949), (1956), Gittenberger, Backhuys and Ripken (1970) and Cameron and Kerney (in preparation). *Helicodiscus singleyanus* has a flattish shell (with a depressed spire) consisting of up to four whorls and reaching a diameter of 2.4 mm and a height of 0.9 mm. The shell is thin, fairly translucent and whitish in colour. The whorls are tightly coiled with deep sutures and there is a large open umbilicus on the ventral side. The surface of the shell (like that of *Vitrea*) is glossy and only weakly marked with axial growth lines: in this respect it contrasts with the two British species of the Endodontidae which have strong axial sculpture on the shell.

A North American species *Hawaii miniscula* (Binney) can also be confused with *Helicodiscus singleyanus* and there are records of *Hawaii miniscula* introduced into Europe where it has been found in greenhouses (Kuiper 1956). Altena (1961) did discover further specimens of *Helicodiscus* labelled as *Hawaii miniscula* in a museum collection and it is likely that other European specimens have been similarly misidentified. Although *Helicodiscus singleyanus* and *Hawaii miniscula* are likely to be confused as shells, they are readily separable on the radula (Kuiper 1956) if the animal is present.

The species *Helicodiscus singleyanus* has been divided into two sub-species, but Pilsbry (1948) reports that they are very similar and in practice, most difficult to separate. *H. singleyanus inermis* H.B. Baker was originally described from North American material (Baker 1929). This sub-species reaches a smaller size (2.2 mm compared with 2.4 shell diameter) and has no, or less well marked, spiral lines on the shell when compared with the typical form of *H. singleyanus*. Previous authors (Kuiper 1956, Altena 1961, Gittenberger, Backhuys and Ripken 1970) have assigned all European records of this snail to the sub-species *inermis*. As there were no distinct spiral lines on the shells examined from Britain, these must be *H. singleyanus inermis* also.

DISCUSSION

As a number of discoveries of *H. singleyanus* have been made in Europe in recent years, it seems likely that this snail has been overlooked both in surveys in North America

and in Europe. More records are to be expected in the future especially through the examination of samples of leaf litter, soil or shell-sand from rivers. There has even been one record of the shell of this snail from a seashore strandline at the Hook of Holland (Schmid 1970).

Most of the published records of *H. singleyanus* in both North America and Europe are based on dead shells found in stream debris or leaf litter and almost nothing is known about the living snail in its natural habitat. One report of a living specimen (Pilsbry 1948) describes the animal and also refers to its collection from roots and bulbs in a Californian garden. Various references in the literature (Pilsbry 1948; Kuiper 1949, 1956; Kadolsky 1967 and Gittenberger, Backhuys and Ripken 1970) point towards a damp habitat of a woodland or marshy area. The concensus of opinion is that this is a subterranean snail, like *Ceciliodes acicula* (Müller), and because of this it would be easily overlooked and difficult to find in the living state. Being a subterranean snail it is possibly one which is not well adapted to withstand dry conditions. Kuiper (1949, 1956) records empty shells of *Helicodiscus singleyanus* in walls in a dry habitat in Switzerland, but these were dead shells and it is possible that living snails could find a moist situation deep within a wall where soil pockets might have accumulated. Whilst some of the European records of *Helicodiscus* came from the countryside, others were from disturbed or artificial habitats. Schmid (1969) published a record of this snail from pot plants in a house in Germany.

Whether *H. singleyanus* in Europe is an introduced species or an overlooked native snail is unresolved. Some of the European sites in which it has been found, like Kew Gardens, Surrey, would suggest an introduction. However other sites where the snail has been found are in more remote areas and these are not so easy to explain. The single fossil record (although only one shell) from the Pleistocene of Czechoslovakia does lend some support to the idea of a native origin for *Helicodiscus* in Europe, perhaps supplemented by some introductions from North America.

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ADDENDA

1. Since the submission of this paper, more soil samples from the archaeological excavation at La Bergerie, Jersey have been sieved and sorted by the Rev. G. Long. A total of 11 further specimens of *Helicodiscus singleyanus* were extracted from three soil samples taken from varying parts of the site. These shells were of various stages of growth and in some the periostracum was present. *H. singleyanus* was the only species of mollusc found in these samples.
2. In November 1976 some land shells were brought to the Academy of Natural Sciences, Philadelphia, U.S.A. for identification. These 5 shells were all *Helicodiscus singleyanus* and they came from an archaeological excavation of an 18th century privy conducted by Historic Deerfield Inc., Deerfield, Franklin County, Massachusetts, U.S.A. This extends the known range of the snail in North America.

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GEOGRAPHICAL DISTRIBUTION OF *POTAMOPYRGUS JENKINSI* (SMITH 1889) (PROSOBRANCHIA: HYDROBIIDAE) IN SPAIN

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Abstract: A survey was carried out in the Granadian Depression to determine the existence of *P. jenkinsi* (Smith), which resulted in the discovery of five new locations. Localities in which *P. jenkinsi* did not occur are also recorded.

A bibliographical summary of its geographical distribution in Spain is given. Finally we consider that a more detailed study is necessary to determine its precise locations and a subsequent comparative study after many years to show that this species is, in fact, spreading in Spain.

Resumen: Se ha realizado un estudio en la Depresión de Granada para determinar si existe en ella *P. jenkinsi* (Smith), encontrando dicha especie en 5 nuevas localidades.

Así mismo, se ha llevado a cabo una revisión bibliográfica para establecer la distribución de este molusco en España.

Se considera, por último, que antes de hablar de dispersión de *P. jenkinsi* en España, debe hacerse un estudio detallado para localizar los lugares en que se encuentra actualmente, estudio que debe repetirse después de varios años para observar si se han producido modificaciones, obteniéndose solamente entonces los datos necesarios para considerar si existe o no dispersión de esta especie en España.

Since the discovery of this species for the first time in the outskirts of London, many articles have been published on its origin, taxonomic position, morphology, etc., although the greatest number of works is dedicated to its distribution throughout Europe, e.g. Berner (1959 and 1963), Fretter and Graham (1962), Hunter and Warwick (1957), Lucas (1963 and 1965) and Real (1973).

Knowledge of the geographical distribution of *P. jenkinsi* in Spain is limited for the moment to various references, chiefly by Spanish writers, to different provinces. Having collected it for the first time in Andalucía, we think it is interesting to compile these data to give a total picture of its actual distribution in Spain.

Continuing, the references made by the different authors are indicated chronologically, noting that the U.T.M. co-ordinates have been assigned to them, showing the places to within 10 km.

Boettger (1951) published the first data on *P. jenkinsi* in Spain, in Catalonia (outskirts of Barcelona: 31TDF28), proceeding with a collection which he himself had made, in 1947; however, in the collection in the Zoology Museum in Barcelona, there exist samples gathered by Gasull in 1936 from some canals close to the airfield of Muntadas, Prat de Llobregat, Barcelona (31TDF27), although this locality was not published.

Altimira (1960) found it in the province of Barcelona: Casa Antúnez (31TDF27), Prat de Llobregat (31TDF27), Gavá (31TDF17), Castelldefels (31TDF16), Vallvidrera (31TDF28), Rubí (31TDF19) and Las Planas (note: the only place we found of this name is in the province of Gerona, very near to that of Barcelona; its co-ordinates are: 31TDG65).

Lucas (1963) gathered it from along the Cantabrian shore, in the following places:

province of Guipúzcoa: Guetaria (30TWN69), Zumaya (30TWN59) and river Urola (Cestona) (30TWN68); province of Vizcaya: Durango (30TWN27); province of Santander: estuary of the river Aguerra (Oriñón) (30TVP70), Escalante (Santoña) (30TVP51), tributary of the river Pas (Torrelavega) (30TVN19), Cobreces (Comillas) (30TVP00), Oyambre (Comillas) (30TUP90), tributary of the river Saja (Ucieda) (30TUN99), Riente (30TUN99) and tributary of the river Besaya (Barros) (30TVN19); province of Asturias: estuary of the river Canero (Luarca) (29TQJ02); province of La Coruña: estuary of Pasajes (La Coruña) (29TNH49).

Gasull (1966) found numerous colonies in different places in the province of Alicante: La Alcudia, Carrizales and Valverde (Elche) (30SYH03), Aspe (30SXH94) and Dolores (30SXH92), collecting only samples with smooth shells.

Altimira (1968) collected it in the province of Gerona, from the pond of Màs Turía (Castelló de Ampurias) (31TEG07).

Vilella (1968) found very numerous colonies in the province of Lérida, in the river Sed (Alfés) (31TCG00).

Altimira (1969) gathered it from the estuary of Navia (Navia, Asturias) (29TPJ82) and the delta of the river Llobregat (Barcelona): Cornellá (31TDF27), San Boi (31TDF27) and Viladecans (31TDF17). In this same publication there is a reference to *P. jenkinsi carinatus* (Marshall), found together with the normal form in La Podrida (31TDF27).

Gasull (1971) found it in the following places: province of Alicante: in the places already mentioned by him in 1966 and in Campaneta (on the road from Almoradí, km 4) (30SXH82), San Isidro and Canales (Albatera) (30SXH82) and Mudamiento (30SXH81); province of Valencia: canal at Ranés (Cerdá) (30SYJ11); province of Murcia: Monteagudo (30SXH60), Casillas (30SXH71), Fuente Alamo (30SXG67), river Mula (Alguazas) (30SXH51), Cruz Quebrada (Murcia) (30SXH60), Molina de Segura (30SXH51), Cehégín (30SXH01) and Archena (30SXH41).

Altimira and Balcells (1972) came across examples in a canal beside the railway-station at Tardienta (Huesca) (30TYM05).

Real (1973), in addition to compiling a great quantity of data on its polymorphism, ecology, biological cycle, etc., indicates on his map D the distribution of *P. jenkinsi* in Spain in 1968, omitting, however, the province of Alicante, which had already been referred to by Gasull in 1966, and marking all the coastal area of the Cantabric, although mention has only been made of some.

Gasull (1974) collected it in the province of Castellón de la Plana: Peñíscola (31TBE77) and Burriana (30SYK41).

Bech (1974) found it in the following places: province of Lérida: canal at La Mallola, canal at Màs de Cal Carreter and canal at Pantà de Les Malloles (Alamús) (31TCG10); province of Tarragona: swamps of Cunit (31TCF86); province of Barcelona: canal at Can Tunis and torrent of Tres Serres (outskirts of Barcelona). It has been impossible for us to find the last two localities on the maps consulted therefore we were not able to indicate the U.T.M. co-ordinates.

During several collections of molluscs carried out in the years 1974 and 1975 in the Granadian Depression and its surroundings, many examples of *P. jenkinsi* of the normal kind (smooth shell) were found.

Since, according to our bibliography, the species has never been found in Andalucía, we consider these references very important for a knowledge of its distribution throughout the Iberian Peninsula. Out of all the localities studied (shown in Fig. 1), this species appeared only in the following:

A canal in the crossing to Villanueva de Mesía: 30SVG1117 (500 m altitude).

Fuente del Tejo: 30SVG5524 (1250 m altitude).

A canal 1 km from Maitena: 30SVG6212 (1100 m altitude).

Stream Aguas Blancas: 30SVG6319 (1120 m altitude).

A canal in El Padul: 30SVF4496 (750 m altitude).



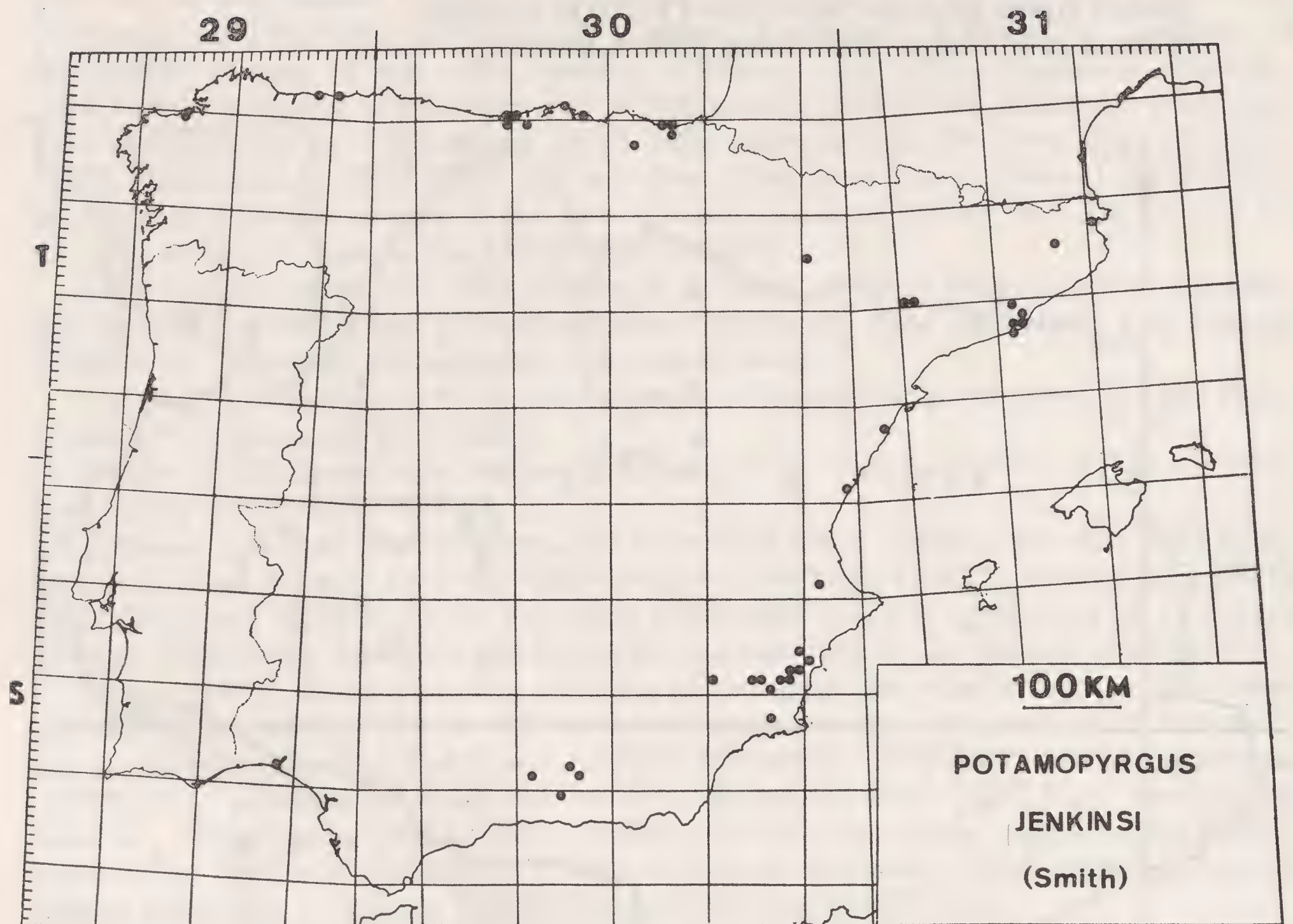
Fig. 1. Distribution of *P. jenkinsi* in the Granadian Depression and its surroundings.

According to these data, the distribution of *P. jenkinsi* in Spain is as indicated in Fig. 2; and as can be seen the actual known distribution is almost restricted to coastal regions, both Atlantic and Mediterranean. *P. jenkinsi* has not been cited yet in the centre of Spain.

DISCUSSION

The dispersion of *P. jenkinsi* throughout Europe has been followed step by step and attempts made to ascertain its ways of invasion and the manner in which they were effected. The most widespread hypothesis indicates that it reached England from New Zealand, then scattering, born by aquatic birds, to the rest of Europe; nevertheless, some authors hold different views, like Margalef (1974), who points out that 'En los moluscos, de los que suelen existir colecciones, resulta más fácil preferir la explicación de una rápida dispersión a suponer que lo que ha ocurrido ha sido simplemente darse cuenta de algo que ya existía. Pero siempre es sospechosa la tendencia a situar en países lejanos el origen de especies cuya aparición resulta misteriosa'.

Due to these contradictory views, we consider it necessary to make more intensive

Fig. 2. Distribution of *P. jenkinsi* in Spain.

investigations to clarify the question completely. Even though the most widely held opinion among malacologists is that it is of foreign origin, a hypothesis supported by the works of Winterbourn (1970–1972), which show morphological and biological similarities exist between *P. jenkinsi*, the European species, and *P. antipodarum* (Gray), the New Zealand species, the data that exist in Spain on the distribution of this species are not sufficient to suppose that a dispersion of *P. jenkinsi* is taking place. In reality the areas in which it has been found are precisely those in which the most intensive investigations have been carried out.

We think that the only convincing way of showing the dispersion of this species in Spain consists of effecting a detailed study to find out its exact distribution at the present time and a subsequent study after several years to observe any changes, having then sufficient information to speak about the dispersion of *P. jenkinsi*; for that reason the locations in which this species have been found are shown in Fig. 1, as well as all those places which have proven negative (the latter are indicated in the appendix).

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APPENDIX

Localities in the Granadian Depression in which *P. jenkinsi* has not been found; its co-ordinates to be taken as U.T.M. (they are all situated in the area 30S) and their altitude is given in metres.

1. UG9212 – 520 m	32. VG3734 – 680 m	63. VG6013 – 1140 m
2. UG9814 – 460 m	33. VG3819 – 580 m	64. VG6311 – 920 m
3. UG9919 – 760 m	34. VG3931 – 710 m	65. VG6311 – 1080 m
4. VG0314 – 480 m	35. VG3924 – 650 m	66. VG6421 – 1150 m
5. VG0413 – 500 m	36. VG4030 – 720 m	67. VG6410 – 1340 m
6. VG0716 – 490 m	37. VG4027 – 700 m	68. VG6409 – 1380 m
7. VG1030 – 880 m	38. VG4016 – 600 m	69. VG6509 – 1390 m
8. VG1018 – 500 m	39. VG4204 – 770 m	70. VG6621 – 1200 m
9. VG1225 – 800 m	40. VG4619 – 720 m	71. VG6601 – 2870 m
10. VG1207 – 700 m	41. VG4604 – 800 m	72. VG6700 – 3040 m
11. VG1202 – 740 m	42. VG4603 – 860 m	73. VG6920 – 1320 m
12. VG1316 – 550 m	43. VG4731 – 700 m	74. VG6900 – 3040 m
13. VG1313 – 530 m	44. VG4714 – 760 m	75. VF0890 – 980 m
14. VG1422 – 580 m	45. VG4841 – 930 m	76. VF1194 – 1060 m
15. VG1516 – 560 m	46. VG4824 – 980 m	77. VF1294 – 900 m
16. VG1923 – 630 m	47. VG4926 – 1060 m	78. VF1296 – 810 m
17. VG2126 – 700 m	48. VG4925 – 1000 m	79. VF1982 – 1230 m
18. VG2416 – 550 m	49. VG4923 – 1100 m	80. VF2280 – 1100 m
19. VG2517 – 530 m	50. VG5113 – 720 m	81. VF2389 – 840 m
20. VG2602 – 860 m	51. VG5212 – 720 m	82. VF2384 – 930 m
21. VG2916 – 550 m	52. VG5205 – 1260 m	83. VF2490 – 860 m
22. VG3130 – 620 m	53. VG5413 – 750 m	84. VF4693 – 740 m
23. VG3124 – 560 m	54. VG5404 – 1350 m	85. VF4794 – 780 m
24. VG3120 – 540 m	55. VG5504 – 1420 m	86. VF4791 – 750 m
25. VG3118 – 550 m	56. VG5615 – 800 m	87. VF5991 – 1700 m
26. VG3423 – 600 m	57. VG5712 – 1000 m	88. VF6391 – 1760 m
27. VG3419 – 560 m	58. VG5704 – 1600 m	89. VF6391 – 1740 m
28. VG3521 – 580 m	59. VG5816 – 920 m	90. VF6391 – 1763 m
29. VG3519 – 570 m	60. VG5810 – 1500 m	91. VF6990 – 1840 m
30. VG3618 – 580 m	61. VG5906 – 1460 m	
31. VG3617 – 580 m	62. VG6013 – 1100 m	

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AN INVESTIGATION OF VARIATION IN
SHELL FORM IN *DISCULA* (*HYSTRICELLA*)
TURRICULA (LOWE, 1831) (PULMONATA:
HELICACEA)

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(Read before the Society, 15 January 1976)

Abstract: Measurement of samples of *Discula turricula* collected over a long span of time from Ilheu de Cima, Porto Santo, indicated that from around 1900 the mean spire height had decreased to a new stable value, the change being accompanied by a temporary increase in variance of shell shape. This change was possibly caused by an alteration in micro-climate following the construction of a lighthouse on the islet in 1900.

Discula (*Hystricella*) *turricula* (Lowe 1831) is a small, turreted snail found only on the Ilheu de Cima, an islet in the Madeiran archipelago. Ilheu de Cima or Upper Island (also called Ilheu do Farol, Lighthouse Island) lies some 400 m. off the south-east point of Porto Santo, which latter island is some 42 km. north-east of Madeira. A fierce riptide runs over the submarine ledge joining Ilheu de Cima to the main island and may well help to account for the endemic nature of the non-marine molluscan fauna of the islet. The flat top of Ilheu de Cima is some 120 m. above sea level and bears a manned lighthouse; access to the top of the islet is made relatively easy by the steps leading to the lighthouse. The top of the islet is covered with quite dense thickets of sapling trees and bushes, but with a sparse ground cover of lichens, moss and *Mesembryanthemum*. *Discula turricula* abounds under the numerous large basaltic lumps that litter the top.

In 1970 I visited Ilheu de Cima for one day, as part of a much longer field-trip to the archipelago (Pettitt 1977), when I collected a sample of *D. turricula*. Fifty years earlier, in 1920, Prof. Cockerell had visited the islet and in 1922 he published a note on *D. turricula* in which he commented that his sample displayed a great variability of shell form. Prof. Cockerell remarked that from genetic theory he would have expected a small, long-isolated population such as this to become uniform in its characters, even if originally variable; this would only be so, of course, if the selective pressures on the population remained constant, which initially seemed a reasonable assumption. What was intriguing, however, was that my own 1970 sample did not display this variability but appeared quite uniform in shell shape.

I therefore obtained the loan of a sample of Prof. Cockerell's shells from Colorado University Museum and compared them with those I collected. I also examined a sample from the collection of the Manchester Museum and two samples found in the Museo Municipal in Funchal, Madeira. Several further samples, from the Salisbury collection in the Royal Scottish Museum, Edinburgh, were looked at also, but most lots were of only 2-3 shells and were without provenance, although one lot of ten shells had a label indicating that it was a mixture of Lowe and Cockerell shells. Because of their uncertain collecting dates these samples were not included in the analysis.

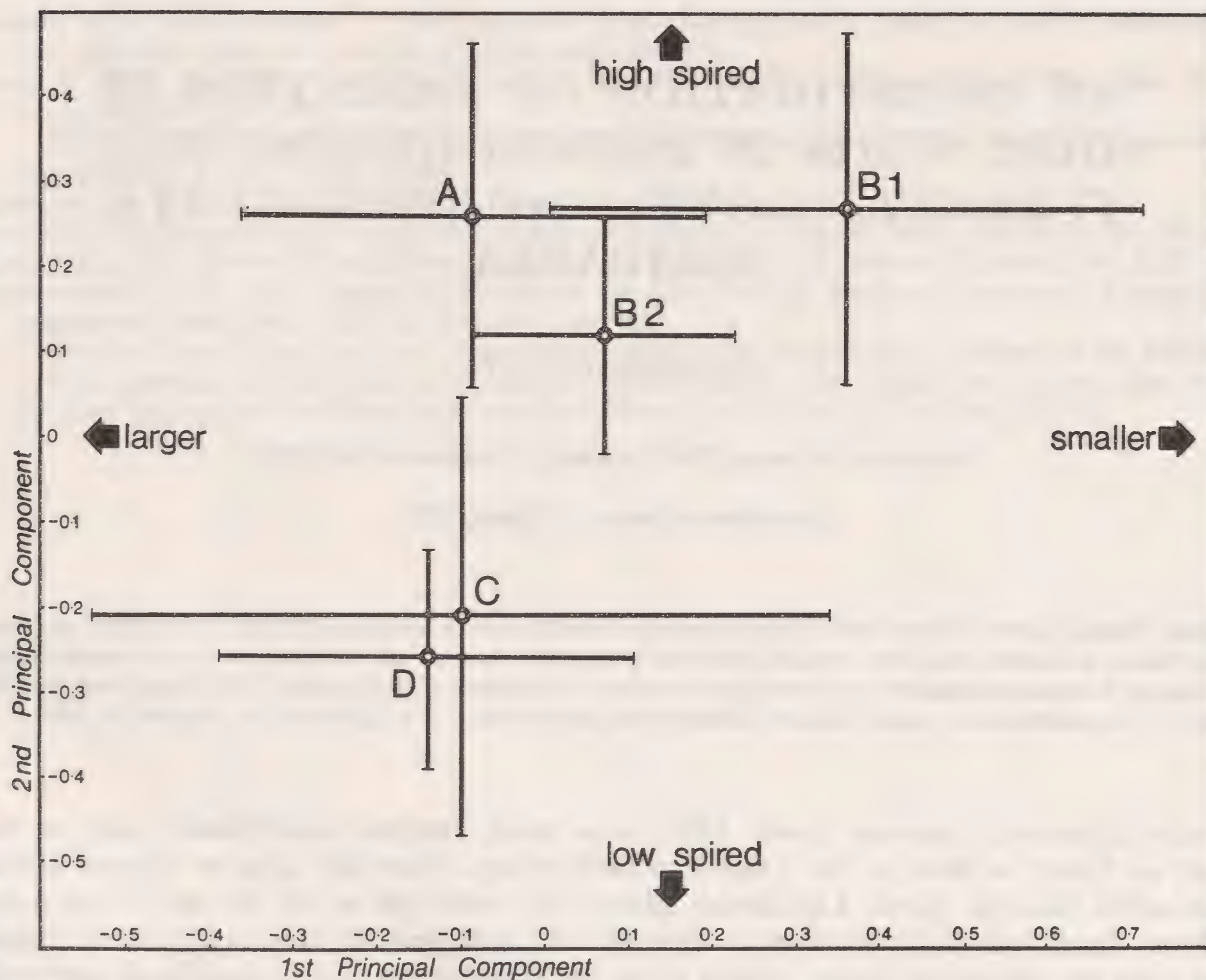


Fig. 1. Mean and $2 \times$ standard error of 1st and 2nd principal components of shell shape in *D. turricula*. For details of the five samples A–D, see text.

The total shell height, maximum shell breadth (across the thickened lip) and shell diameter at right angles to the aperture were measured to 0.1 mm. using vernier calipers; only adult shells with fully thickened lips were scored. These three measurements were subjected to a principal components analysis for me by Dr. L. M. Cook, following the method of Seal (1964). The resulting first and second principal components are plotted on Fig. 1, where it will be seen that the samples tend to form two clusters, with the samples A, B1 and B2 in one cluster and samples C and D in another.

Sample A is from the Layard collection in the Manchester Museum, which must have been collected no later than 1899, for Layard died on the 1 January 1900, and his collection was purchased that year by Manchester Museum. In all probability it was collected much earlier; although an active collector in the southern hemisphere Layard never collected in the Madeiran archipelago, but from his retirement in 1890 until his death he greatly extended his collection by exchange (Collier, 1900). One of the people with whom he is known to have exchanged was Wollaston, and it is therefore likely that it was from him that Layard obtained the *Discula turricula*; this would mean that they were almost certainly collected in the period 1830–1855 by either Lowe or Wollaston (Wollaston, 1878). Samples B1 and B2 are from the Funchal Museum and were almost certainly collected by Noronha within the period 1900–1920 (G. E. Maul, *in litt.*); as two separate lots were present, it may be supposed they were collected on separate occasions, although unfortunately the samples are undated. Sample C was collected by Prof. Cockerell in 1920 and sample D by me in 1970. The first principal component may

be interpreted as a measure of the overall size of the animals, and the second a measure of the shell shape, particularly spire height. The analysis seems therefore to indicate that between the collection of the second of Noronha's samples and Prof. Cockerell's visit the animals had become slightly larger and there was a change in mean shell shape from a higher- to a lower-spired form.

I then calculated the variance of the angular transformation (θ) of the ratio of shell breadth (measured at right angles to the aperture) to shell height (Table 1). The significance of the resulting variance ratios for each pair of samples (F-statistic) was then determined (Table 2). Because the standard errors shown in Fig. 1 are influenced by sample size they differ in relative magnitude from the variances in Table 1. The inference may be drawn from the figures, however, that from 1845 to around 1900 the population was stable and of uniform shell shape (samples A, B1), but that sometime around 1900–1910 the mean spire height of the population tended to decrease (sample B2). At the time Cockerell took his sample (C) there was increased variability and the mean spire height was already significantly lower than before; finally, my sample may record a new equilibrium reached by a population which is again fairly uniform.

TABLE 1

Means and variances of the samples of *Discula turricula*

Sample	N	Mean B/H	Mean θ	Variance	Date collected
A	12	0.697	56.59	7.000	1855*
B1	11	0.695	56.50	4.800	1900–1920*
B2	39	0.709	57.35	12.404	1900–1920*
C	20	0.746	59.76	14.939	1920
D	25	0.746	59.74	5.540	1970

* See text for details.

TABLE 2

Variance ratios (F-statistic) and associated probabilities (P) for the samples of *D. turricula*

Samples	B1		B2		C		D	
	F	P	F	P	F	P	F	P
A	1.458	NS	1.772	NS	2.134	0.1	1.264	NS
B1			2.584	0.05	3.112	0.05	1.154	NS
B2					1.204	NS	2.239	0.05
C							2.697	0.01

Shell dimensions are in part inherited but may also be strongly influenced by ecological factors (Cook and O'Donald 1971). One may therefore conclude that around the turn of the century some kind of disturbance probably occurred which altered the environment and resulted in a ecological and/or genetic response by the snails; it could well be that this change coincided with the building in 1900 of the lighthouse on Ilheu de Cima. For it seems reasonable to suppose that the erection of this fairly massive lighthouse and its attendant buildings which, together with its service road running the width of the plateau, occupies a significant area of the islet, would have caused not only short term disruption during the building work, but could have changed permanently the micro-climate of the islet surface. The wives, children and domestic animals of the keepers also live in the lighthouse complex and this population of a previously uninhabited islet may

well have significantly altered the vegetation pattern on the plateau, again with repercussions upon the micro-habitat of *D. turricula*. It is possible that the total effect of these changes has been to cause the selection of a broader, lower-spired animal than before as the type best fitted to the new environment.

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A REVIEW OF *PLEUROBRANCHELLA* THIELE, 1925 (OPISTHOBRANCHIA: PLEUROBRANCHAEINAE)

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(Read before the Society, 18 December 1976)

Abstract: *Pleurobranchella* (= *Pleurobranchoides* O'Donoghue, 1929; *Gigantonotum* Guang-Yu and Si, 1965) contains possibly four described species, all known only from preserved material collected from depths greater than 200 m. The genus is characterized by a large mantle which overhangs the foot laterally and posteriorly and by simple lateral teeth in the radula. A revised definition of *Pleurobranchella* is presented, together with brief descriptions of all known species.

As part of a taxonomic review of the New Zealand members of the opisthobranch order Notaspidea the writer has attempted to re-evaluate proposed genera. This paper presents results for one genus, *Pleurobranchella* Thiele, 1925. It is published separately because this genus has not been found in New Zealand waters.

Pleurobranchella belongs within the notaspidean subfamily Pleurobranchaeinae as defined by Odhner (1926); the other two genera contained are *Pleurobranchaea* Meckel in Leue, 1813 and *Euselenops* Pilsbry, 1896. In external form *Pleurobranchella* resembles both *Euselenops* and *Pleurobranchaea*; all three have the mantle confluent with the oral veil anteriorly, but *Pleurobranchella* differs in having a very large mantle which covers the foot laterally and posteriorly. O'Donoghue's description (1929: 62) of the mantle in *Pleurobranchella gilchristi* applies suitably to all members of the genus *Pleurobranchella*: 'The mantle has a wide outstanding margin all round, so wide that it extends beyond the foot and in the dropped position touches the substratum outside the foot, thus enclosing a very large sub-mantle cavity which is equally developed all round'. In *Pleurobranchaea* the mantle is reduced and, in some species, confluent with the hind end of the foot. *Pleurobranchella* lacks a pedal gland, this gland is present in adult *Pleurobranchaea*. Internally the most important difference is that in *Pleurobranchella* the lateral teeth are simple, lacking the secondary denticle found in *Pleurobranchaea*. The reproductive system of *Pleurobranchella* has a prostate gland as in *Pleurobranchaea*, and a papillose penis as in *Euselenops*.

GENUS *PLEUROBRANCHELLA* THIELE, 1925

Pleurobranchella Thiele, 1925, *Wiss. Ergebn. dt. Tiefsee-Exped. 'Valdivia'*. Gastropoda in Tiel II: 149. Type species by monotypy *Pleurobranchella nicobarica* Thiele, 1925.

Synonymy – 1929. *Pleurobranchoides* O'Donoghue, *Union of South Africa, Fisheries and Marine Biol. Survey* 7(1): 62. Type species by original designation *Pleurobranchoides gilchristi* O'Donoghue, 1929.

1965. *Gigantonotum* Guang-Yu and Si, *Oceanologia et Limnologia Sinica* 7(3): 270; 276. Type species by original designation *Gigantonotum album* Guang-Yu and Si, 1965.

Each of the above descriptions adequately defines this single genus. The latter two have been proposed in ignorance of the pre-existing available genus.

Thiele (1925) distinguished *Pleurobranchella* from *Euselenops* Pilsbry by the much larger mantle of the former which completely overlies the foot posteriorly. Thiele commented that the rhinophores arise from a deep sinus on either side between the mantle and oral veil. Thiele suggested *Pleurobranchella* could be a subgenus of *Euselenops*. The description of *Pleurobranchella* is accompanied by illustrations of the buccal mass, a lateral view of a jaw element and radular teeth, although no radular formula was given. I have redrawn Thiele's radular figures (Fig. 1). O'Donoghue (1929) gave a detailed account of *Pleurobranchoides gilchristi*, including figures of mandibular elements and radular teeth, he also illustrated abnormal teeth which were interpreted as having resulted from fusion of two separate teeth. Guang-Yu and Si (1965) again emphasized the great development of the mantle in relation to the foot and compared *Gigantonotum* with *Koonsia* Verrill, 1882. Guang-Yu and Si gave illustrations of jaw elements and radular teeth, also dorsal and ventral views of the preserved holotype are given in a coloured plate.

A definition of the genus *Pleurobranchella* can be presented by amalgamating the information from all three proposed genera.

Pleurobranchella Thiele, 1925. Pleurobranchs of large size, body oval and inflated, blunt anteriorly; mantle and oral veil larger than foot, mantle overhanging foot laterally and posteriorly, merging anteriorly with oral veil; rhinophores far apart, mantle with a distinct shoulder behind rhinophore; oral veil with weak tubercles along anterior border; pedal gland and caudal spur absent; gill rachis tuberculate, anus above gill half way along fixed portion of rachis; lateral teeth of radula without an accessory denticle; mandibular elements polygonal, denticulate along anterior edge; penis papillose, prostate present.

A few authors have subsequently mentioned *Pleurobranchella* or its synonyms. Odhner (1926) had presumably not seen Thiele's description, because *Pleurobranchella* is absent from Odhner's 'Synopsis of the types and classification of the Pleurobranchidae'. In 1931 Thiele himself placed *Pleurobranchella* as a subgenus of *Euselenops*. Eales (1938) described a damaged specimen, details of the jaws, radula and reproductive system are given. For comparison Eales (1937) examined the type specimens of *Pleurobranchoides gilchristi* O'Donoghue and in the crop of the larger specimen (66 mm long) were fourteen juvenile *Pleurobranchaea capensis* Vayssi re. Burn (1962) listed only *Pleurobranchoides*. Marcus and Marcus (1970) felt that *Pleurobranchella* could hardly be distinguished from *Pleurobranchoides* and noted the resemblance to *Gigantonotum*.

The genus *Koonsia* Verrill, 1882 (type species by monotypy *K. obesa* Verrill) can be compared with *Pleurobranchella*. In the original description Verrill (1882, p. 545) states '... back swollen and overhanging both on the sides and posteriorly, and a distinct mantle-edge all round, as well as laterally'. Solely on this description *Koonsia* might well be taken as congeneric with *Pleurobranchella*. But fortunately Verrill (1885) subsequently published an illustration of *Koonsia obesa* which was later reproduced by Pilsbry (1896). The figure is of a species of *Pleurobranchaea*, indeed Vayssi re (1901, pp. 72-3) compares it with *Pleurobranchaea meckelii*. Preservation has caused contraction of the body resulting in the appearance of the mantle being separated from the foot all round (even anteriorly from the oral veil), but the illustration shows a very small mantle. The rhinophores are close together and not separated from the mantle or oral veil by a groove. To add to this conclusion, are Verrill's comments that the head, rhinophores, oral tube and gill agree with those of *Pleurobranchaea*. He describes a posterior ventral pedal gland on the foot and a dorsal caudal spur, neither of which have been seen in *Pleurobranchella*.

Pilsbry (1896, p. 221) repeated Verrill's description of *Koonsia* and placed *Pleurobranchillus* Bergh, 1892 (type species *P. morosus* Bergh) as a synonym. Vayssi  re (1901, p. 22) treated both *Koonsia* and *Pleurobranchillus* as belonging to *Pleurobranchaea*, remarking however, that studies of internal anatomy could reveal generic differences. I follow Vayssi  re in viewing both genera as junior synonyms of *Pleurobranchaea* Meckel in Leue.

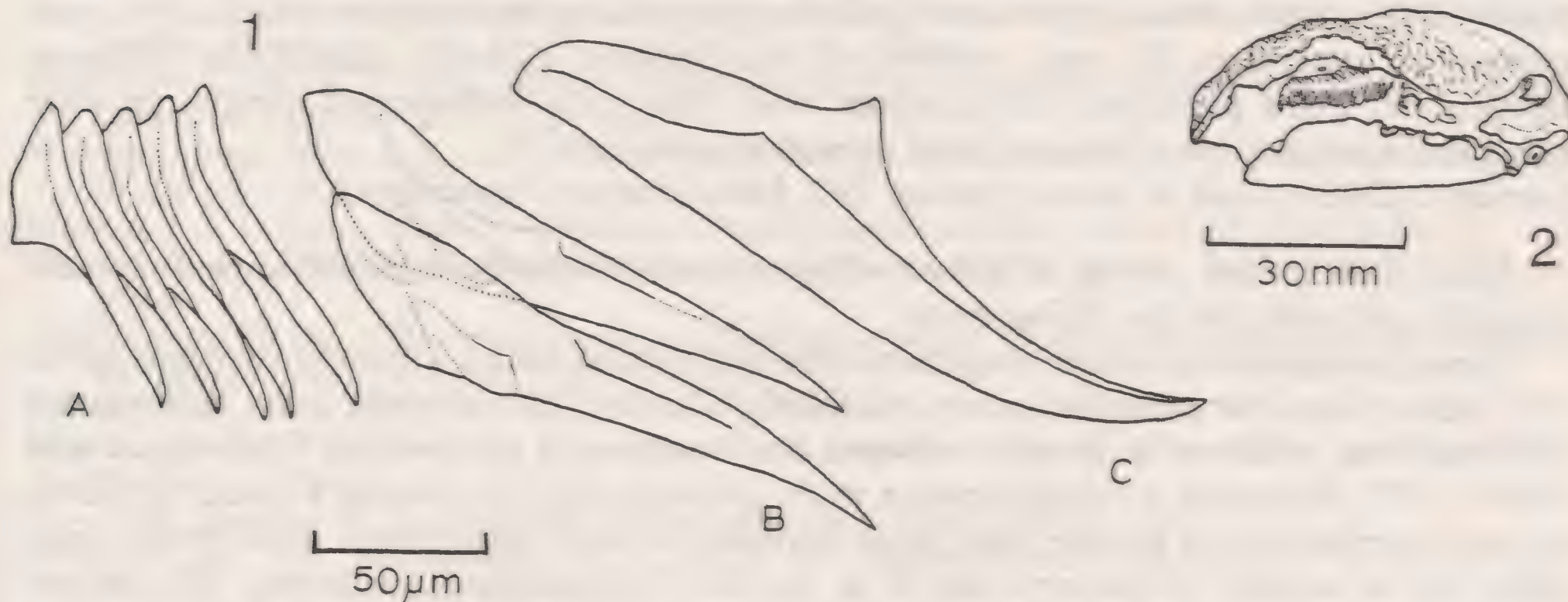


Fig. 1. Radular teeth of *Pleurobranchella nicobarica* Thiele; A, inner laterals; B, middle laterals; C, outer laterals. Redrawn from Thiele, 1925. Fig. 2. *Pleurobranchella gilchristi*: lateral view. Redrawn from Eales, 1937.

Four described species can be included in *Pleurobranchella*. A summary of specific characters is given below. Since only Eales (1938) has compared her specimen with *Pleurobranchella gilchristi* (O'Donoghue), and no critical comparisons have been made by previous authors (O'Donoghue 1929; Guang-Yu and Si 1965) a full comparison and specific evaluation remain to be undertaken. It is possible that some of these species are the same.

1. *Pleurobranchella nicobarica* Thiele 1925. Colour? Penis constricted, spiral and contorted, the tip having two different faces; one long, concave and smooth, the other shorter and convex, with numerous sharp tubercles. Radular formula? Inner lateral teeth very small, teeth becoming larger away from the centre; blades narrow, weakly curved (preserved material only, three specimens).

Type locality: 269 m; S.W. of Great Nicobar Island, Indian Ocean.

2. *Pleurobranchella gilchristi* (O'Donoghue 1929). Mantle soft and smooth, greyish-white in colour with sole of foot, sides of body, gills and everted reproductive organs fawn grey. 38 pinnae on each side of gill. Radular formula $34 \times 110.0.110$, inner laterals small, lanceolate and pointed, middle lateral teeth larger and slightly curved, outermost teeth consist of a thin, small, roughly rectangular base with a long finger-shaped cusp rising from one corner. Reproductive organs surrounded by a 2–3 mm high membranous collar, penis with a stout, cylindrical base bearing a very long, cylindrical, blunt ended portion, the end is covered with a large number of minute tubercles (preserved material only, two specimens).

Type locality: 343 m; off the South African Coast.

3. *Pleurobranchella alba* (Guang-Yu and Si 1965). Mantle smooth dorsally, with numerous small pustules ventrally; mantle greyish-white, gill and sole of foot yellowish orange. Gill attached for two thirds of its length with 32 pinnae on each side. Radular formula $52 \times 144.1.144$, central conical, lateral teeth hook-like, the first lateral slender, second

and third like scales, larger towards the middle, the outermost teeth slender; mandibular elements apparently not denticulate. Penis cylindro-conical (preserved material only, one specimen).

Type locality: 220 m; south of Hainan Island, China.

4. *Pleurobranchella* sp. (Eales 1938). Mantle smooth (but wrinkled due to contraction). Colour? Radular formula $40 \times 120.0.120$; laterals all alike, increasing in size for two-thirds of the distance from the centre and then decreasing, base narrow blades erect and triangular, outermost 20 teeth curved on the radular ribbon; mandibular elements denticulate. Penis papillose, but unarmed and lying in a well-formed sheath, prostate small and compact (one damaged and preserved specimen).

Locality: 220 m; Gulf of Aden (Station 194, John Murray Expedition).

Since descriptions are all of preserved specimens, details of external appearance are probably not exact for the living state.

Some inconsistencies concerning characters that can be used for specific determinations are evident from the published accounts. Firstly Thiele (1925) described the rhinophores as rising from a furrow or groove between the mantle and oral veil in *P. nicobarica* and Eales (1937) illustrates a similar groove in *P. gilchristi* (Fig. 2). Guang-Yu and Si (1965) do not describe such a groove, and none is visible in their illustration. This groove may either be an artifact of preservation or a specific distinguishing character. The second inconsistency concerns the radula. A rachidian is present in *Pleurobranchella alba* (Guang-Yu and Si 1965), but apparently not present in either *P. gilchristi* (O'Donoghue 1929) or the specimen examined by Eales (1938). It is possible that the rachidian teeth are vestigial in *Pleurobranchella* (as they are in *Pleurobranchaea*) and hence teeth from this row in *Pleurobranchella* are also liable to be lost in preparation or overlooked during examination.

REMARKS

All species of *Pleurobranchella* appear to be confined to deep seas, at depths greater than 200 m. O'Donoghue (1929) felt *Pleurobranchella* to be intermediate in some respects between *Pleurobranchus* and *Pleurobranchaea*, but overall closer to the latter. The only genuine similarity between *Pleurobranchus* and *Pleurobranchella* is the large mantle which covers the foot, in most characters *Pleurobranchella* is much closer to genera of the subfamily Pleurobranchaeinae. *Pleurobranchella* shows the anterior fusion of mantle and oral veil and consequent rhinophoral separation that is found only in *Pleurobranchaea* and *Euselenops* amongst notaspidean genera. *Pleurobranchella* may be ancestral to each of these genera, having given rise to both lines independently. In both genera there has been a reduction in mantle size; *Euselenops* retaining a separate and distinct mantle border laterally and behind, and in *Pleurobranchaea* there is sometimes posterior fusion of mantle and foot. *Pleurobranchella* apparently displays the actively roving predatory habit (as evidenced by Eales' (1937) observations) which is conspicuous in species of *Pleurobranchaea* (e.g. *P. novaezelandiae*, personal observation). Therefore *Pleurobranchella* may be existing at present as a deep water relict genus.

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SOME OBSERVATIONS ON THE GROWTH OF THE COMMON DOG-WHELK, *NUCELLA LAPILLUS* (PROSOBRANCHIA: MURICACEA) IN THE LABORATORY

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(Read before the Society, 18 December 1976)

Abstract: It has generally been assumed that *Nucella lapillus* reaches maturity after three years, and that the adult shell does not increase in size or change shape thereafter. Most European populations reach an adult shell length of 2.5-3.5 cm, but in the Bristol Channel lives a larger form which commonly exceeds 5.0 cm. Despite high mortality rates, attempts to breed the large form in the laboratory indicate that newly hatched snails had shells shorter and squatter than those of their parents. Some juveniles grew quickly in their second year, passing the 'normal' adult size of 3 cm in 18 months and two laid egg capsules at 19 months. Had they continued to grow at the same rate these juveniles would have reached parental size and shape in 3 years. However, most of the young snails grew more slowly and showed no sign of ever reaching large size. Successful rearing of *Nucella* in aquaria seems to require circulation of water and temperatures below 25°C.

The Common Dog-Whelk, *Nucella lapillus*, is a predatory marine snail widely distributed along the rocky shores of the North Atlantic (Cooke 1915). It feeds predominantly on acorn barnacles and mussels and is almost confined to the inter-tidal zone. The eggs are laid in capsules, attached to the rock surface and the young hatch directly as tiny snails without any intermediate planktonic stage. The young are carnivorous from birth, feeding on serpulid worms of the genus *Spirorbis* if they are available, but on barnacles or other molluscs if not (Largen 1967a). It is generally thought (Moore 1936, Feare 1970) that the young take three years to reach sexual maturity and that all shell growth takes place during this immature phase. Adults are thought not to increase in size.

In south-west Britain, and probably over most of the species' range, the mean adult length (height) is between 2.5 and 3.5 cms. The shells vary in shape in a remarkably predictable manner according to the degree of exposure of the shore to wave-action. A survey of shell-shape in Pembrokeshire (Crothers 1973) produced a relationship of

$$Y = 1.214 + 0.036 X$$

where Y is a measure of shell shape (length divided by aperture length) and X is the exposure of the shore on Ballantine's (1961) exposure scale. Subsequent computations using data from Brittany, Norway, Devon and Cornwall as well as Pembrokeshire have slightly modified this to

$$Y = 1.217 + 0.035 X$$

which is not significantly different from the original. I am indebted to Dr. W. J. Syrratt for this formula.

In the Bristol Channel this relationship breaks down. All the populations examined (Crothers 1974) had much more elongated shells with mean Length:Aperture Length ratios in excess of 1.60, and there is no obvious correlation between shell shape and exposure to wave action. In the transition zone between the 'normal' western form and the 'elongated' Bristol Channel form there occurs a large race of *Nucella lapillus* in which shells are frequently longer than 5.0 cms. They are usually markedly elongated, with length:aperture ratios between 1.75 and 1.80.

The experiments described in this paper were intended to establish the growth pattern of this large form. In particular I wished to discover whether

- (a) the large form bred true
- (b) they achieved their size by growing faster than 'normal' snails
- or (c) by growing for a longer period.

It is difficult to find juvenile *Nucella* on some Bristol Channel shores and I decided to carry out this work in laboratory aquaria.

MATERIAL AND METHODS

Trial 1 (1972/1973). A dozen adult *Nucella*, of the large form, were collected from the lower shore at Gore Point (Porlock Bay) on 16 March 1972 and kept in an aquarium tank. A total of 85 egg capsules were laid, the first on 28 March and the last on 29 April. 902 juveniles hatched from these capsules in a two-month period starting on 28 June, mostly in mid July. It is difficult to measure but easy to damage newly hatched *Nucella* so the young snails were left undisturbed in their tank until early October. The sea water was aerated continually but not changed during this period, and the snails were provided with a supply of the acorn barnacles *Elminius modestus* and *Balanus balanoides* for food.

Initial mortality was heavy and only 107 were alive on 12 October. These survivors were measured to the nearest 0.1 mm using a vernier calliper, and a mean figure obtained for the length:aperture length ratio (see Crothers 1973, 1974, 1975a, b). These measurements were repeated at two monthly intervals when the water and barnacle-covered rocks were renewed.

Most of the young snails survived the winter of 1972-73 but the death rate rose again to a high level during the following summer and only two individuals were alive in October. In nearly every case the young snails died as a result of losing their shells. Opinions as to the reason for this were many and various but possibly it was in some way due to their being raised in still water.

Trial 2 (1974-1976). During the winter of 1973-74 I modified my aquaria to a re-circulating system with the animals kept in tidal tanks. The tides are of short duration (about 20 mins) but it was considered that the stimulus of moving water and fluctuating levels was of more importance than the natural tidal cycle.

Twenty-three adult *Nucella* of the large form were collected from Gore Point on 23 February 1974. The first egg-capsules were noted on 21 March and the animals continued to lay until early May. The first embryos again hatched in late June with the main emergence between 8 and 15 July. The tidal range in the tanks was adjusted so that the capsules were permanently submerged as Feare (1970) reported that such capsules were more likely to hatch.

By September, when the young snails were large enough to measure, there were 560 survivors. These were distributed amongst four tanks and measured at monthly intervals. Once again there was a high initial death rate, with a number of accidental losses each time the rocks were changed. Very few lost their shells and there were still 360 alive in May 1975. Then the hot summer took its toll.

Largen (1967b) found that *Nucella* became inactive at 25°C and entered heat coma if kept at 27°C. The shade air temperature at Nettlecombe rose above 25° on thirteen days and above 27° on five, reaching over 30°C on two consecutive days in August. Over 300 young *Nucella* died during this hot weather. Very few lost their shells. And the last survivors died during the hottest weather of the 1976 summer.

CROTHERS: GROWTH OF *NUCELLA LAPILLUS*

TABLE 2

The Growth of aquarium-raised dog-whelks, *Nucella lapillus*: Trial 2

Date measured	n	Mean L (cms)	Mean L of the five biggest (cms)	L of the biggest shell (cms)	Mean L/Ap
September 1974	560	0.64	1.25	1.30	1.41 \pm 0.06
October 1974	480	0.82	1.50	1.58	1.42 \pm 0.06
November 1974	477	1.00	1.73	1.79	1.415 \pm 0.06
December 1974	460	1.08	1.99	2.13	1.425 \pm 0.06
January 1975	441	1.14	2.13	2.26	1.43 \pm 0.06
February 1975	384	1.19	2.20	2.37	1.42 \pm 0.06
March 1975	383	1.23	2.21	2.37	1.435 \pm 0.06
April 1975	372	1.24	2.22	2.36	1.43 \pm 0.05
May 1975	359	1.30	2.22	2.36	1.43 \pm 0.055
June 1975	300	1.44	2.36	2.61	1.44 \pm 0.06
July 1975	204	1.50	2.58	2.61	1.465 \pm 0.07
August 1975	54	1.75	2.57	2.67	1.48 \pm 0.07
September 1975	27	2.00	2.74	2.90	1.52
October 1975	17	2.25	2.91	3.29	1.55
November 1975	9	2.59	2.94	3.32	1.57
December 1975	7	2.70	2.95	3.38	1.57
January 1976	6	2.71	2.84	3.41	1.57
February 1976	4	2.87	—	3.43	1.60
March 1976	4	2.87	—	3.49	1.62
April 1976	3	3.20	—	3.55	1.60
May 1976	3	3.21	—	3.57	1.61
June 1976	3	3.29	—	3.70	1.62
July 1976	1	3.70	—	3.70	1.66

No survivors in August 1976.

The animals were not always all measured on the same day, but in the first week of the month indicated

TABLE 1

The growth of aquarium-raised dog-whelks, *Nucella lapillus*: Trial 1

Date measured	n (number alive)	L (length) (cms)	L/Ap (length:aperture length)
12.10.72	107	0.67	1.42 \pm 0.06
15.12.72	89	0.88	1.41 \pm 0.04
13. 2.73	78	1.02	1.42 \pm 0.05
12. 4.73	66	1.13	1.44 \pm 0.04
13. 6.73	53	1.24	1.44 \pm 0.05
15. 8.73	14	1.31	1.44
25.10.73	2	1.28	1.48
12.12.73	3	1.27	1.48
14. 2.74	3	1.31	1.48
11. 4.74	3	1.48	1.48
18. 6.74	3	1.50	1.44
12. 8.74	3	1.56	1.47
10. 9.74	2	1.61	1.55

No survivors in November 1974.

RESULTS

The changes in size and shape of the growing *Nucella* are set out in the Tables and Figures. The Trial 2 animals clearly grew slightly faster (Fig. 1) than their predecessors kept in still water, but after 11 months there was very little between them. So few of the

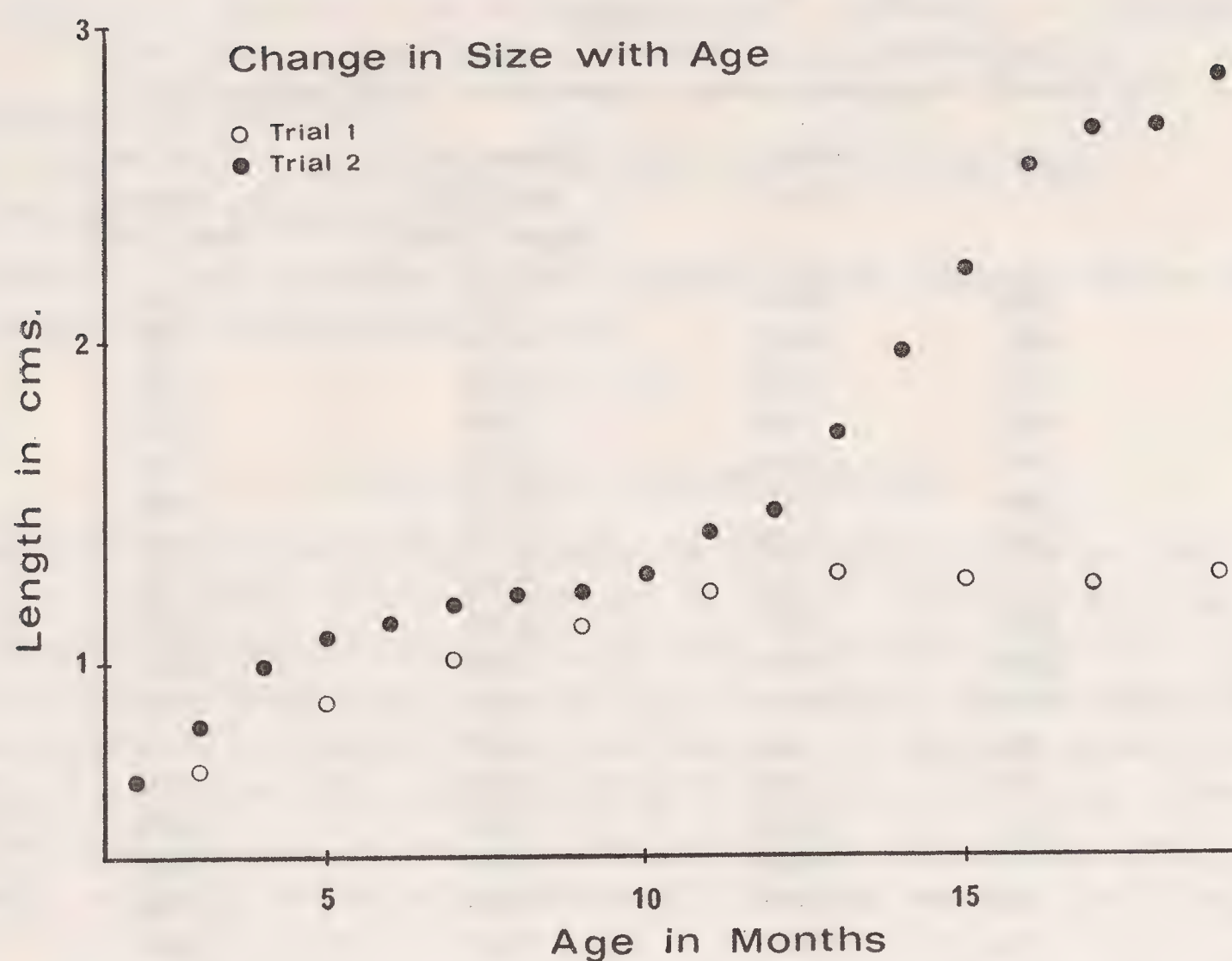


Fig. 1. The increase of shell length (height) of aquarium raised dog-whelks with age. Trial 1 refers to 1972-74 and Trial 2 to 1974-76. The age is given in months after hatching from the egg-capsules (July) so that month 5 is December. The points indicate mean values and thus are less meaningful after the thirteenth month as the number of surviving animals is small in each trial.

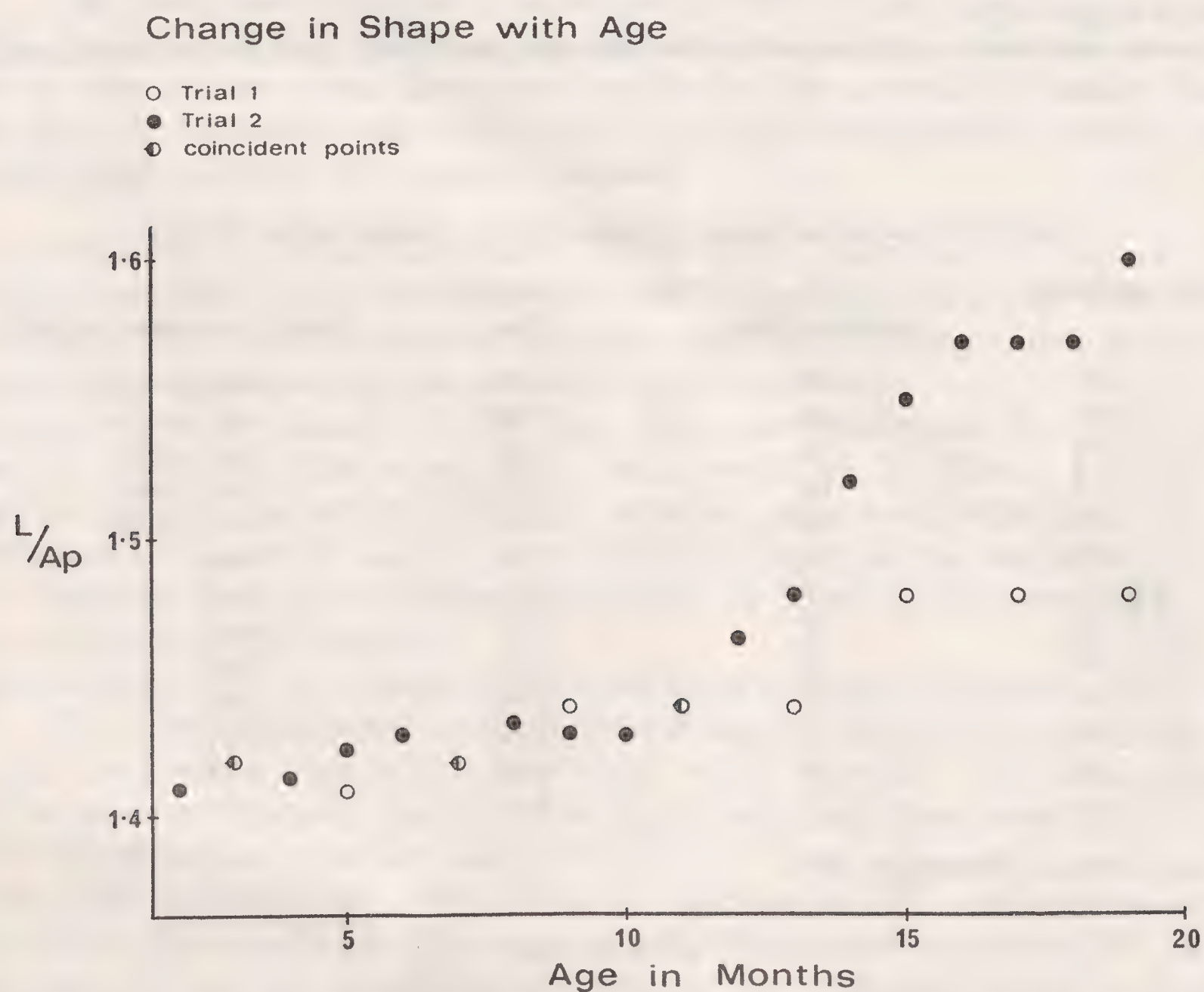


Fig. 2. The change in shell shape, as indicated by length divided by aperture length, of aquarium raised dog-whelks with age. Trials 1 and 2 and age as in Figure 1.

DISCUSSION

Despite the unsatisfactory nature of the data presented in this paper due to the high death rate amongst the experimental animals, it is apparent that some offspring of the large form of *Nucella lapillus* have the ability to grow large like their parents, and that they achieve this size by growing faster rather than by growing for longer than normal. The largest ones reached the 'normal' adult size of 3 cms within 18 months of hatching and were clearly on their way to developing their parents' elongated shape, all of which suggests a genetic influence on both the rate of growth and the adult size and shape.

It is also clear that only a minority of the original progeny would have shown this pattern, for most of them grew much more slowly and remained shorter and squatter until they died. Table 2 shows the differences in size between the 5 largest animals and the mean for the whole trial.

The shells of the young dog-whelks in their first year were of the shape to be expected (from the equation on p. 157) on a shore of exposure of 5–6 on the Ballantine scale. The most exposed ridge of Gore Point rates as exposure 4 (Crothers 1976) and the actual site whence the parental snails were collected is about 5, so that the young animals grew 'normally' to start with and only began to develop an elongated 'Bristol Channel' form during their second year. This allometric growth pattern was not expected and further experiments are in progress to see whether this occurs in other populations.

The attempt at breeding when the young snails reached 'normal' adult size but only 19 months after hatching was also unexpected. Moore (1936, 1938) had concluded that sexual maturity was reached at an age of $2\frac{1}{2}$ –3 years and that it coincided with cessation of shell growth. Mature shells could be recognized by their thickened lip and by a row of white 'teeth' along the inside of the lip. The formation of these features is actually indicative of the cessation in growth rather than maturity (Cowell and Crothers 1970) but it has usually been assumed (e.g. by Feare 1970) that growth did indeed stop on maturity. The animals in Trial 2 continued to grow after laying their capsules and neither layed down 'teeth' nor thickened the shell lip.

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REVIEWS

Living Marine Molluscs. By C. M. Yonge and T. E. Thompson. 288 pp. 16 plates, 165 text figs. Collins London. 1976. Price £6.00.

The ever increasing mountain of marine molluscan literature has for some time demanded a more popular review. The majority of this book is written by Sir Maurice Yonge and I can think of few people better qualified to attempt such a task. The resulting book is both readable and very informative.

As the title suggests the book attempts to deal with all marine molluscs. The approach is largely taxonomic with each class being examined individually. The Monoplacophora (deep sea, limpet-shaped molluscs) and Aplacophora (very small, worm-like molluscs) are merely mentioned while the more common Polyplacophora (coat-of-mail shells), Scaphopoda (elephant tusk shells) and Cephalopoda (octopods, cuttlefish and squids) are given more detailed treatment. The majority of the book is devoted to the more abundant and diverse Gastropoda (7 chapters) and Bivalvia (5 chapters). They are each introduced by a chapter on their possible origin and evolution. The gastropods are then dealt with by order and the bivalves according to their mode of life. These chapters attempt to put the 'flesh' on the bare shell of taxonomy by describing the general ecology of different groups by reference to individual species.

The introduction makes it plain that this is not a book for those interested purely in the molluscan shell. Although the shell is often described, it is viewed more as an accessory enclosing the main centre of interest, and is only really appreciated when its design has some ecological significance. Emphasis is fortunately placed on the distribution and function of the internal organs without digressing into detailed descriptions which would be inappropriate in a book of this kind.

The specific examples used to illustrate the groups are drawn from the authors' own experience and this results in a predominance of well researched British species. This is reflected in the appearance of many familiar figures from the British literature. Hardly a page passes without a diagram (165 in all). These are clear, concise and economical in space although some of the more detailed anatomical illustrations have suffered slightly from reduction. I particularly appreciated the completeness of the captions which remove the necessity of interrupting the text with detailed explanations. The 16 pages of plates are divided equally between monochrome and colour. They are well selected except that the sea slugs, because of their spectacular shape and characteristic colours, might have benefited from greater coverage. This could have been achieved by treating a number of plates in monochrome, e.g. *Eledone cirrhosa* (plate 12) and omitting altogether the pointless picture of *Anomia ephippium* (plate 11).

The only major reservation I have about this book is its intended readership. It is probably not of interest to the general reader but is more suited to the student or serious amateur, whose appetite will be whetted for further reading. Although there is a short, comprehensive book list there are no references within the text itself. Personally I find it irritating to be denied access to the wealth of accumulated knowledge of the authors especially when the nuggets of information are hinted at in the acknowledgements to text figures. I realise that this is not an uncommon practice and that acknowledgements are necessary, however, detailed references, either in the caption or preferably included in a separate comprehensive bibliography, would immeasurably increase the value of the book. Such a list could have been partially accommodated by omitting the photograph acknowledgements which are to a great extent already covered by the captions themselves.

This book is in many ways similar to that by J. E. Morton (*Molluscs*. Hutchinson University Library London, 1958, 232 pp.). It too was an attempt to give an up-to-date, synoptic view of molluscs (although it also included land and freshwater ones). Yonge and Thompson have cited more species in detail and have increased the number and quality of illustrations, but they have omitted the detailed references (nearly 300) included by Morton. It is perhaps unfair to compare the two books too closely because Morton adopted a morphological rather than taxonomic approach, so that, in many ways, the books complement each other.

To conclude, this book contains a great deal of well illustrated information and is an essential addition to the bookshelf of those interested in molluscs. I can certainly agree that it is 'an important contribution to the literature of malacology by two of the foremost authorities on their subjects'.

P. F. LINGWOOD

REVIEWS

Framgälade snäckor från Svenska västkusten [Prosobranch snails from the Swedish west coast]. By Bengt Hubendick and Anders Wären. Naturhistoriska Museet, Göteborg. 1976. Price 25 Swedish kronor.

This slim volume is a must for those who work on the North Atlantic fauna. The book is a series of seven papers published in the *Göteborgs Naturhistoriska Museum Årstryck* between 1969 and 1975 which have been put together with an introduction and a list of the names of the species covered.

The alphabetical list of specific and generic names, valid and synonyms, follows the short introduction. The synonyms refer the reader to the valid names which are linked to the figures and the text by the figure number. This is most necessary as the pages are still numbered as they were in the *Årstryck* which causes confusion at first glance. The name list functions then as an index. Species additional to those figured and described are included in the name list, for example, the British *Alvania carinata* (da Costa).

The fairly conservative nomenclature used follows the *Concordance** for the most part, but does sometimes include names used on the Continent. For example, *Onoba striata* (Montagu) appears in the descriptive part but is included in the name list as *Onoba semicostata* (Montagu) and *O. striata* is listed in the synonyms. *Eulima bilineata* (Alder) is used instead of our accepted *E. trifasciata* (Adams). Hubendick and Wären place *Cingula cingillus* (Montagu, 1803) in the synonymy of *C. trifasciata* (J. Adams, 1800), a change already hinted at by Nordsieck (1972)†, but here dated 1898, a mistake presumably, for 1798. It can be irritating to find that the older usage, for example *Nassarius* in the text has been replaced in the name list by *Hinia*. Again *Omalogyra* appears with an initial *H* in the text but has been corrected in the name list. However this sort of anomaly should not present any problems to those familiar with British nomenclature.

The largest part of the work consists of brief descriptions of the species plus geographical distribution, depth range and substrate. The Swedish text is not too difficult to cope with; *Inledning* is clearly *inleading* or introduction, and *Alphabetisk lista över namn* needs no translation. Most of the technical terms are Latin with Swedish suffixes and are immediately comprehensible. After translating *Framgälade snäckor* as *forward gilled snails* a mood of confidence was established.

The superbly executed, large drawings are the *raison d'être* of the book. There are usually two views of each species, more where the species is particularly variable, like *Rissoa parva*. Juveniles, protoconchs and details of sculpture are figured where this aids identification.

One hundred and forty-eight small recent and fossil prosobranch species which are found, or are likely to be found, in the Kattegat and Skagerrak are described. 101 of the species covered are included in the *Concordance**, and so can be considered as part of the British fauna. Many of these species are the less common northern ones which appear so rarely in popular works on British molluscs. The Rissoidae are covered quite extensively and well, but an expert would wonder about the identification of the shells illustrated in figures 63–71 as *Rissoa lilacina* Desmarest. Only figures 64 and 69 can objectively be identified with Desmarest's ribbed and punctate species, while the rest appear to be the ribless and punctate *Rissoa porifera* Lovén. In the final *Remarks and corrections* several identification mistakes are corrected. So that the reader will not miss these the whole section is translated and reproduced below.

Alvania abyssicola (Forbes) Figs. 3–4. The species so described is *A. subsoluta* (Aradas). Each of the names have been shown to represent valid species. The species characteristics for *A. abyssicola* correspond to the shell in figs. 283–284.

Alvania castanea (Möller) Figs. 14–15 are not *A. castanea* but are *A. mighelsi* (Stimpson). *Alvania* or *Cingula castanea* is known only from the Arctic Ocean, not from Scandinavia. *Onoba proxima* (Forbes & Hanley) figs. 75–76. Continuing studies on all Nordic material in Scandinavian museums which have been called *O. proxima* show that it should be *O. acicula* (Gould). Those figured here are therefore *O. acicula*.

Hemialcis. The names have been switched. Figs. 149–150 represents *H. ventrosa* Jeffreys and 151–152 is *H. glabra* Sars. The size of the shell in figs. 151–152 is two millimetres.

Lora bicarinata (Couthouy) (Fig. 231) One living specimen was found at Säcken, N. Bohuslan, during the summer of 1974.

Erato voluta (Montagu) (fig. 118). Found at Grimstad on the Norwegian Skagerrak coast, 1974.

The book can be ordered from Naturhistoriska Museet, Box 11049, 40030 Göteborg, Sweden for 25 Swedish kronor. A cheque should accompany the order.

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† Nordsieck, F. 1972. *Die europäischen Meeresschnecken (Opisthobranchia mit Pyramidellidae: Rissoacea)*. Gustav Fischer, Stuttgart.

British Land Snails. Synopses of the British fauna (new series) No. 6. By R. A. D. Cameron and Margaret Redfern. vi+64 pp., 31 figures. Linnean Society and Academic Press. 1976. Price £1.90.

British land snails, as the title implies, covers terrestrial gastropods with shells, including the two prosobranch species and 85 pulmonates. Land slugs are not included. The early sections succinctly cover shell structure, basic anatomy, biology, collection and classification of British land snails. A purely artificial dichotomous key is presented, based almost entirely on shell characters. The main part of the booklet is devoted to brief descriptions and figures of the shells of all the species treated. References to recent literature and an index of specific names, including common synonyms, conclude the booklet.

This is a handy guide which I am sure will prove useful in the field and is reasonably priced. While flattering to the Society, it is unfortunate that the nomenclature used is based on the Conchological Society's 1966 Census addenda (Kerney 1966) and has therefore been superseded by the appearance of the Society's new nomenclatural list (Waldén 1976). The recent discovery of *Helicodiscus singleyanus* in Britain has also rendered the coverage incomplete, but such discoveries obviously cannot be foreseen. I could not spot any misprints and factual errors are absolutely minimal. However, *Oxychilus alliarius* is not the only species of *Oxychilus* to produce a garlic smell when provoked (p. 43), *O. helveticus* will also; and *Vitrina pyrenaica* is no longer only known from southern Ireland (p. 48), there are now more records from Ulster than from the rest of Ireland.

The illustrations of shells give only a general idea of each species. An experienced worker will recognize all of them, but a beginner will have difficulty with the more featureless groups. The illustrations of *Carychium* spp. and *Vertigo* spp. are good, but those of the two *Columella* species are virtually identical and do not bring out the critical differences. That of *Ceciloides* appears to represent a juvenile and those of *Succineas* and *Clausilias* are all too similar; the illustration of *Marpessa laminata* gives no indication that the surface is shiny. Few readers will realize that most zonitids have shiny shells and many of the illustrations of helicids are slightly distorted, e.g. *Cepaea nemoralis* (p. 53). The magnifications used vary widely and it is a little disturbing to see *Euconulus fulvus* twice the size of *Fruticicola fruticum* on the same page. Even with scales it is difficult to visualize the correct relative sizes. Since most readers will use the figures first, rather than wade through a key with 86 couplets, the value of this synopsis is reduced somewhat by these weaknesses in the illustrations. This is not to say that the booklet is not useful, it most certainly is and will, I am sure, sell well.

C.R.C.P.

British Opisthobranch Molluscs. Synopses of the British Fauna (new series) No. 8. By T. E. Thompson and Gregory H. Brown. vi+204 pp., 1 colour plate, 105 figures. Linnean Society and Academic Press. 1976. Price £3.50.

Sea-slugs, despite their beauty and fascinating habits, have been a rather neglected group of molluscs largely because of the unavailability of adequate identification aids. This comprehensive, up-to-date and clearly illustrated book has removed that obstacle and should greatly promote the study and recording of sea-slugs and other opisthobranchs.

The first few pages give succinct accounts of structure and biology with labelled diagrams that clearly explain the terms used in the keys and the systematic part. The dichotomous keys, based on external features that can fairly easily be seen with the aid of a good lens, are comparatively easy to follow. However, those who lack the patience to use keys will probably find what they want by thumbing through the clear and well laid out descriptions and illustrations of the systematic part which occupies the great majority of the volume. This section has been so arranged that the descriptions and illustrations are almost always on the same page or on facing pages, and never more than one page apart. Virtually every species of opisthobranch ever found in Britain is described and illustrated. The only exclusions are the pyramidellids and, despite an implication in an advertisement circulated by the Academic Press, the pteropods or 'sea-butterflies'.

The precise but readable descriptions draw attention to the external diagnostic features of each species without needless repetition of minor detail. Shelled species of opisthobranch have both shell and soft parts described. Aesthetically, it is regrettable that economy compelled the illustration of such vivid creatures in black and white. One colour plate of four species provides a tantalizing glimpse of the beauty of sea-slugs. But how refreshing it is to find a book that breaks away from reproducing the century old illustrations of Alder and Hancock with such clear lifelike drawings. Readers of recent parts of this journal will be familiar with examples of Mr. Brown's skill in illustrating sea-slugs. In the volume under review his talent is given full rein in large illustrations, often of full page size, that show every detail with precision. For identification purposes the absence of colour is not a great disadvantage as the colours of many species vary in shade and hue. Our attention is instead turned towards the more reliable structural features, but the often important patterns made by the colours are also clearly shown. More ventral views, especially of the heads of dorids, would have been useful if space had permitted, but it is unreasonable to expect the standards of large monographs from a book of this size and price.

REVIEWS

The work is printed on good quality paper and sturdily sewn into flexible 'waterproof' covers, though the Synopses Editor, perhaps wary of the Trades Description Act and of how slug collectors act, cautions against total immersion in sea water! The few printer's errors, such as 'Goose' for 'Gosse' (p. 68) and '7mm' for '70mm' (p. 24) do not materially detract from its usefulness.

Aqualung divers will find it invaluable, but shore collectors will also find it most useful as half of the 130 species described are to be found between tide marks. Anyone with the slightest interest in British bubble shells or sea-slugs should obtain a copy as it will be the standard identification guide for many years to come.

IAN F. SMITH

Pseudothecosomata, Gymnosomata and Heteropoda. By S. van der Spoel. Bohn, Scheltema and Holkema (Utrecht) 1976. Price \$60.

This is the second of a series of monographs on planktonic molluscs and deals with the taxonomy, zoogeography and morphology of the three groups of molluscs detailed in the title. In addition it brings up to date the first volume of the series, 'Euthecostomata, a group with remarkable developmental stages'.

This book itself largely falls into three parts:

- 1) the taxonomy, zoogeography and morphology of the three groups in the title (some 186 pages);
- 2) a list of the type material of the Pteropoda and Heteropoda (some 40 pages);
- 3) an extensive bibliography of published work on planktonic molluscs (some 60 pages).

In addition there are some 160 pages of illustrations of the various species and maps of their distribution.

By the very nature of the subject matter this book is aimed at the professional biologist interested in the marine planktonic environment and this limited circulation is reflected in the price which will put it beyond the reach of those not closely involved with the group. It will undoubtedly be a useful book for those interested in the taxonomy of this varied and interesting group of molluscs as it not only provides keys and detailed descriptions for the identification of the various species but also attempts to unravel the synonymy which is widespread within these groups.

My major criticisms of this book are of the figures rather than the text. The diagrams of some of the Gymnosomata appear to be little more than amorphous blobs in which the various species characters are difficult to distinguish. These figures would have definitely been enhanced by the inclusion of stylized and simplified line drawings for all the species. It should be pointed out that such drawings are included for some species making their absence all the more obvious for the other species.

DAVID W. MCKAY

A catalogue of collations of works of malacological importance. Western Society of Malacologists, 2nd occasional paper. By George E. Radwin and Eugene V. Coan. 34 pp. August 1976. Price U.S. \$2.50.

Do you know which of the Sowerbys published the 'Conchological Illustrations' and which the 'Mineral Conchology', or the dates of the various parts of the 'Thesaurus Conchyliorum'? More importantly, do you know where to look to find out? If the answer to either question is 'no', you would do well to invest in a copy of what must be one of the most useful guides to the literature of molluscs that has ever appeared. Researchers working with a particular group of molluscs or on a biography publish details of dates of publication, etc. of specific works or authors. Journal editors also provide cumulative indexes for journals periodically. What Radwin and Coan have tried to do is to bring references to all such works together in a single catalogue, the 34 pp. of which contain invaluable source references for works on molluscs from those of the Academy of Natural Sciences, Philadelphia to the Zoological Society of London. Over 140 important malacological works or journals are listed alphabetically by authors' names or journal titles, each entry being followed by a chronological list of collations which refer to it. For example, to answer my first question above:

SOWERBY, G. B. (1st and 2nd of the name).

1834, 41. The Conchological Illustrations (and descriptive catalogue of shells by J. E. Gray), London, pls. 1-200.

Sherborn, C. D. 1909, Malac. Soc. London, Proc. 8 (6): 331-32.

Shaw, H. O. N., 1909. Malac. Soc. London, Proc. 8 (6): 333-40.

Reynell, A., 1910. Malac. Soc. London, Proc. 9 (3): 212-13.

Dall, W. H., 1915. U.S. Nat. Mus., Proc. 48 (2079): 437-40.

Cross references are also given, as for example in scientific voyages, viz.:

SULPHUR, the voyage of H.M.S.

see Hinds, R. B., 1843-44.

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The authors accept that since such collations are so widely scattered through the literature, they will inevitably have missed some. Nevertheless, as a first step towards a complete compilation, this work will prove to be a source one will turn to again and again. For its size and price it must surely be one of the most important aids to malacology ever produced. Copies are available, price \$2.50, from Mr. Merton J. Goldsmith, 1622 N. 20th St., Phoenix, Arizona, 85006, U.S.A. Payment should accompany any order.

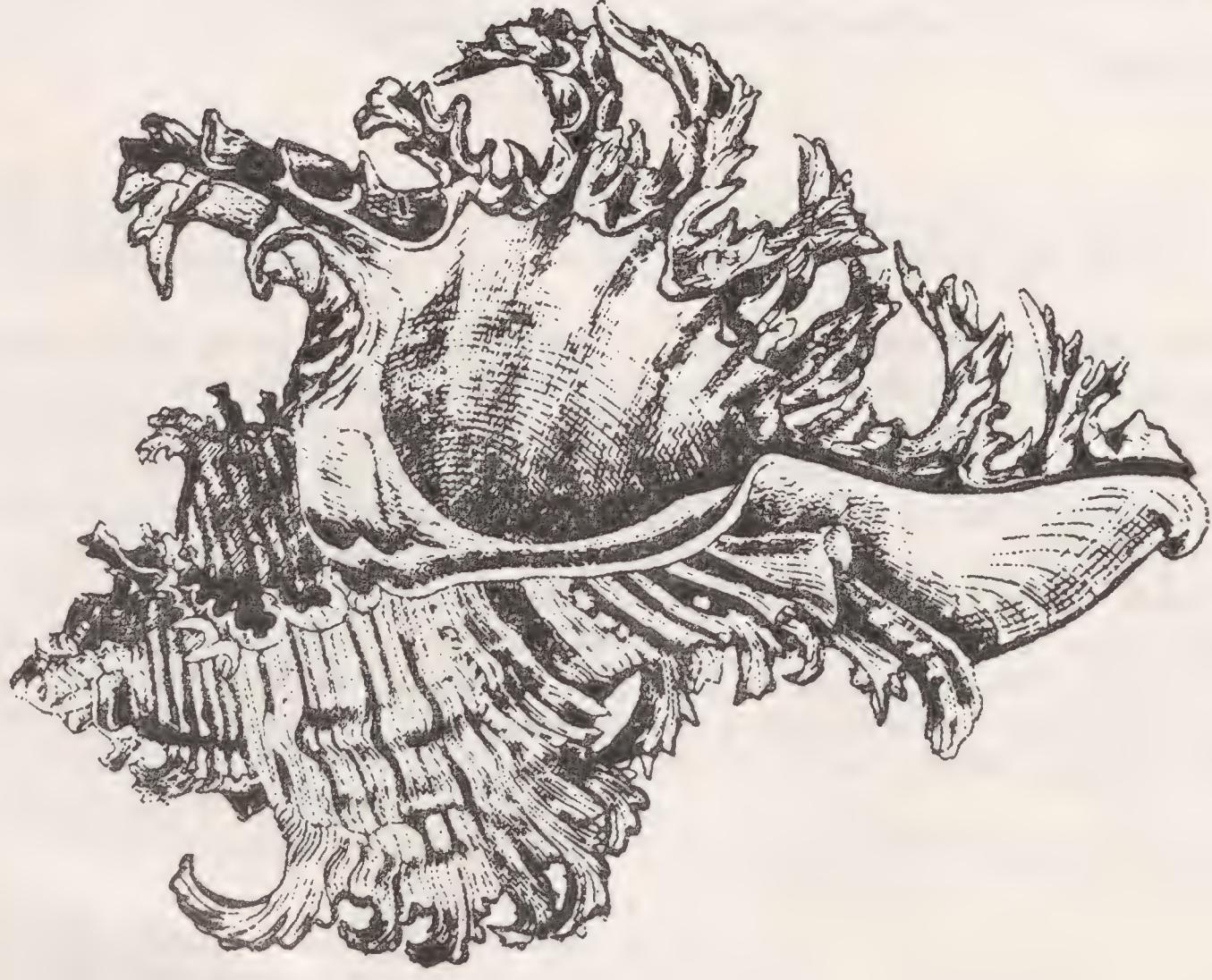
C.R.C.P.



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2. **Two** copies of all text and illustrations should be submitted. (A few years ago the entire copy for one issue of the *Journal* was lost in a mail robbery!). Authors are strongly recommended to retain a further copy for proof correction.

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4. Originals of text-figures should be $1\frac{1}{2}$ –2 times the final size but should not exceed 25 by 36 cm. They should be drawn in Indian ink on clean ground, numbered consecutively, and referred to in the text as "Fig. 1" etc. Authors are strongly urged to construct text-figures so as to make full use of the page width and to submit a copy reduced to final (published) size wherever possible. Lettering should be legible and not less than 1 mm high after reduction.

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For periodicals give full title of the article, title of the periodical abbreviated according to the World List (4th Ed.), volume number, page numbers and plates.

e.g.
WOODWARD, F. R. 1965. Monograph of the British Lower Tertiary Unionidae, with descriptions of three new species. *J. Conch.*, Lond. **25**: 316–330, pls. 22–27.
GOULD, S. J. 1969. An evolutionary microcosm: Pleistocene and Recent history of the land snail *P. (Poecilozonites)* in Bermuda. *Bull. Mus. comp. Zool. Harv.* **138**: 407–532, 5 pls.

8. Authors may obtain copies of all papers (other than brief notes) at cost price if ordered from printers (address: Messrs. Willmer Brothers Ltd., 62–68 Chester Street, Birkenhead, England) when galley proofs are returned.

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Overseas members are reminded that all monies due to the Society are payable in sterling.

TWO LAND SLUGS FROM GIBRALTAR

A. NORRIS
Leeds City Museums

(Read before the Society, 15 January 1977)

Abstract: Details and descriptions are given of *Arion* (*Letourneuxia*) *moreleti* and *Deroceras* (*Malino*) *ponsonbyi* from Gibraltar. The anatomy of the latter is figured for the first time.

Very few species of land slugs are known to occur on Gibraltar. Kobelt's list (1883), one of the few published faunal lists on the Mollusca of Gibraltar, contains only one species *Parmacella calyculata* Sowerby, now considered to be a synonym for *Parmacella valenciennii* Webb and Berthelot. Hesse in his paper on slugs of Tangiers and Gibraltar (Hesse 1884), recorded a number of species from the Rock, several of which were new. A visit to Gibraltar in April 1975 produced six species (Norris 1976), two of which seem never to have been recorded since the original descriptions were published in 1884. Unfortunately, these descriptions are, at least in the case of *Deroceras ponsonbyi* (Hesse), inadequate for modern taxonomic purposes. With the exception of a poor thumb-nail sketch of the genitalia of *Arion moreletti* Hesse, they do not include illustrations of the reproductive organs. The following paper is an attempt to rectify this situation.

DESCRIPTIONS

Arion (*Letourneuxia*) *moreleti* Hesse 1884 = *Arion* (*Ariunculus*) *moreleti* Hesse 1884

Body: the slug is fairly large and robust, 50-55 mm long, 12-14 mm broad, and very similar in appearance to *Arion* (*Mesarion*) *subfuscus* (Draparnaud), particularly in colour. Two well-marked lateral bands occur on the mantle and body, arching just above the respiratory orifice. Above these are two ill-defined dark bands. The mantle is about one-third the length of body, granulose and bluntly rounded behind, with the respiratory orifice slightly in front of centre. The body is rounded behind and without a keel; foot fringe narrow; sole unicolourous, tripartite with a narrow centre section; caudal mucous gland in transverse slit. The shell is oval, solid, convex above, slightly concave below, 5 × 3 mm. Jaw: the odontognath is arcuate crossed by 13 broad ribs, indenting margins, orange-brown. The genital orifice lies below and slants behind the base of the right tentacle, well in front of the respiratory orifice.

Anatomy: The right and left cephalic retractors separate at their origin from the diaphragm; the buccal retractors originate further back near to the midline; the right tentacular branch passes to the left of the genitalia; the genital retractor is inserted into the spermatheca duct. The ovotestis is attached at the base of the albumen gland by means of a long slender hermaphrodite duct. The albumen gland is well-developed, brown, tongue-shaped. The spermovi duct is wrinkled at the upper end becoming more straight, inflated and narrowing to a short oviduct; the vas deferens is attached at the narrowing just above the oviduct. The vas-deferens is swollen for the first half, becoming narrower in the second, attached to about the middle of the epiphallus which is swollen. The spermatheca is bulbous with a short spermatheca duct. The retractor muscle is attached to the base of the oviduct and to the base of the spermatheca duct. The oviduct, spermatheca duct and epiphallus join the atrium separately.

First record: *A. moreleti* was first described by Hesse (1884) on the basis of two specimens of different ages from Tangiers.

Habitat: Common and widely distributed in areas where garden and general debris had been deposited. It is particularly common in Alameda Gardens.

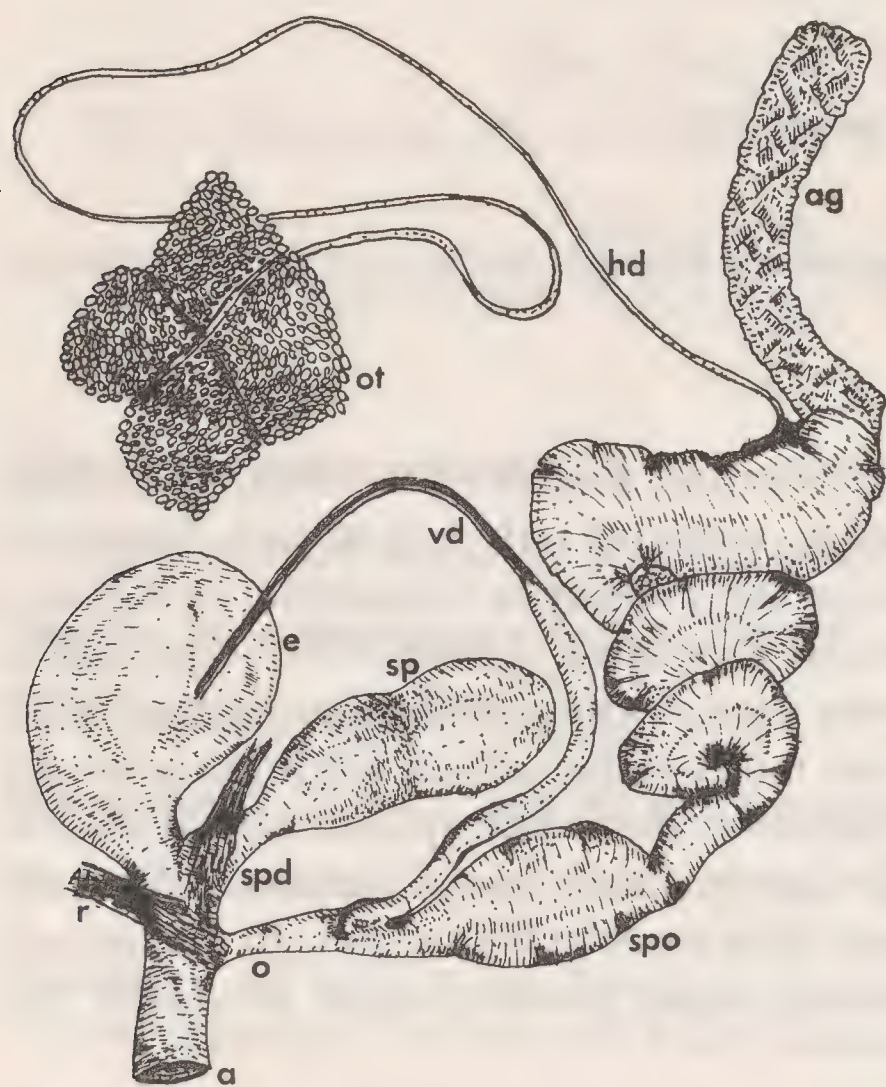


fig.1.

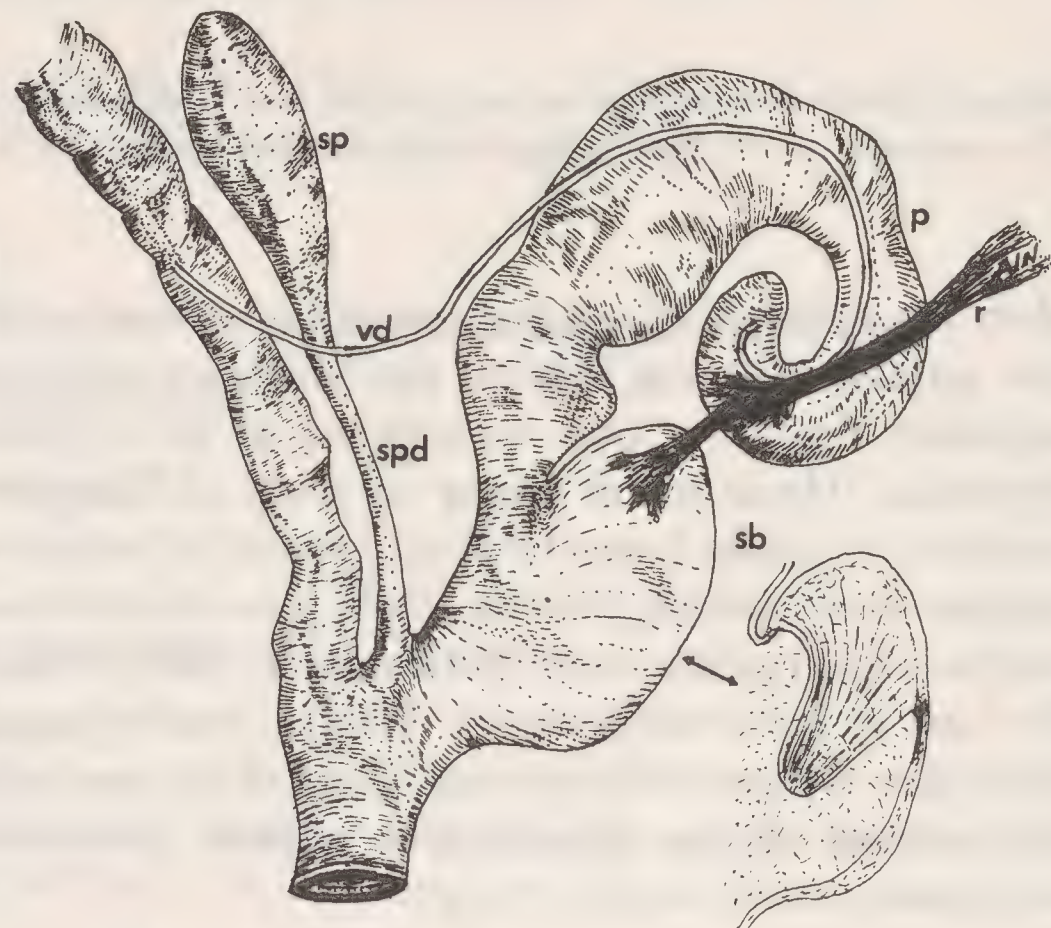


fig.2.

Figure 1. Genital anatomy of *Arion* (*Letourneuxia*) *moreleti* Hesse and of *Deroceras* (*Malino*) *ponsonbyi* Hesse Fig. 2. a atrium, ag albumen gland, e epiphallus, hd hermaphrodite duct, o oviduct, ot ovotestis, p penis, r retractor muscle, sb sarcobelum, sp spermatheca, spd spermatheca duct, spo spermoviduct, vd vas-deferens.

Deroceras (*Malino*) *ponsonbyi* (Hesse 1884) =
Limax (*Agriolimax*) *panormitanus* var. *ponsonbyi* Hesse 1884

Body: The slug is similar in external appearance to a pale mottled form of *Deroceras* (*Malino*) *caruanae* Pollonera, differing in that it has a slight pinkish tinge to its mantle. The body is fractionally larger and heavier than that of *D. caruanae*, 30–35 mm in length. Adults in spirit vary from 20–30 mm. The colour is buff-grey with numerous dark flecks on the body and shield, the slime colourless, the sole tripartite, pale, and the tail abruptly truncated with a short keel. The pneumostome is situated one third from posterior end of the shield. The shell is flat, oval and solid, 4 × 2 mm.

Anatomy: The right ocular retractor passes to the left of the lower genitalia. The genitalia are characterized by a long conical pleated sarcobelum. The penial retractor muscle divides at its attachment to the tip of penis, opposite the entry point of the vas-deferens, and sends a branch which is attached to the part of the penis that contains the sarcobelum. No penial appendage, marked diverticulum, nor rectal caecum, is present.

First record: *D. ponsonbyi* was first described by Hesse (1884) from specimens collected on Gibraltar.

Habitat: It is common under herbage and stones on waste ground and in gardens, always close to human habitation.

NORRIS: TWO SLUGS FROM GIBRALTAR

ACKNOWLEDGEMENTS

I would like to thank the late Dr. C. O. van Regteran Altena for all the help and advice he gave me in tracing the names of the slugs, and for his assistance in the production of this paper. Thanks are also due to Dr. L. Lloyd-Evans without whose help I would never have been able to put pen to paper.

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NOTE ON A CASE OF HOMONYMY IN THE PULMONATE FAMILY STREPTAXIDAE

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Department of Systematic Zoology of the University, c/o Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands

AND

HIROSHI MINATO

Kumano Senior High School, Kamitonda-cho, Wakayama-ken, Japan

(Read before the Society, 16 April 1977)

Abstract: *Gulella* (*Sinoennea*) *insularis* Minato 1974 from Japan is a junior homonym of the West African *Gulella insularis* (Girard 1894). It is suggested that the generic name *Gulella* should be confined to species of the Ethiopian Region. The Japanese species thus becomes *Sinoennea insularis* (Minato) and as such, is allowed to stand.

Recently Minato [1974: (105) 107] described *Gulella* (*Sinoennea*) *insularis* from the Danjo Islets west of Kyushu, Japan. Unfortunately this combination is a junior homonym of *Gulella insularis* (Girard 1894) from Annobon Island in the Gulf of Guinea, West Africa. The species was originally described as *Ennea insularis*. So far this is a straightforward case of secondary homonymy.

However, there is a complication here. Following many authors, but mainly Zilch (1960), Van Bruggen wants to restrict the name *Gulella* L. Pfeiffer 1856, to the species occurring in the Ethiopian Region and adjoining islands as far east as Madagascar, Mauritius, etc. For the Asiatic forms, which are fundamentally different, we follow Zilch and others in using *Sinoennea* Kobelt 1904. The genus *Gulella* is very diverse and has so far been subdivided into a number of subgenera (Zilch 1960: 569 *et seq.*). In future some of these may be raised to generic status. The exact (sub)generic assignment of *Ennea insularis* Girard is still to be decided.

Gulella insularis Minato 1974 thus is a junior homonym of *Gulella insularis* (Girard 1894) (cf. Oztiz de Zárate and Alvarez 1960: 95). However, the Japanese form belongs to *Sinoennea* as defined by Zilch (1960: 573) and therefore should bear the name *Sinoennea insularis* (Minato 1974). Consequently *Gulella insularis* (Girard 1894) and *Sinoennea insularis* (Minato 1974) are allowed to stand as such. The same applies if *Gulella insularis* (Girard 1894) is transferred to another genus, if not *Sinoennea*.

In this context we particularly refer to Article 59 of the International Code of Zoological Nomenclature (1964 edition).

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THE *ARION HORTENSIS* COMPLEX, WITH NOTES ON *A. INTERMEDIUS* NORMAND (PULMONATA: ARIONIDAE)

STELLA M. DAVIES

63 Beechwood Road, S. Croydon, Surrey CR2 0AE

(Read before the Society, 16 April 1977)

Abstract: A general study has revealed three distinct species commonly known as *Arion hortensis* Férussac, here referred to as **A**, **R** and **B**. After observation in natural habitats and in captivity for more than eight years, their essential differences are described, including differences in their external morphology and pigmentation, genital anatomy, shape of spermatophores, and mating behaviour. There is no evidence of interbreeding. In both seasonal and geographical distribution, **A** is the least restricted, and **B** the most restricted of the three species in the British Isles. *A. intermedius* Normand shares the main characters of the group, but critical differences are described.

Evidence is presented that the name *hortensis* Férussac, 1819 should be restricted to species **R**. The correct names for species **A** and **B** remain uncertain pending further research by the author.

The study of an animal as familiar and supposedly well-known as *Arion hortensis* Férussac is far too easily neglected by the ordinary naturalist. The observations described in this paper began by accident, and continued in ways suggested by the slugs themselves.

A large (4 cm) slug, taken inadvertently with a handful of moist woodland leaf-litter from Riddlesdown, Surrey, in November 1967, was left in a jam-jar, and was not noticed until four days later, when it was laying eggs at the side of the jar. After 52 days the eggs showed clear red spots, and the young slugs, which hatched in varying shades of grey down to pure white, all had pink tentacles which darkened gradually with the development of black pigment. This culture was labelled **R**.

In February 1968, another 4 cm woodland slug, found at Wilmslow, Cheshire, was taken deliberately, for comparison with **R**. No red colour was seen in any of its eggs or young.

In April 1968, a first attempt was made to examine *A. hortensis* in a garden at Sanderstead, Surrey. None was found approaching the woodland slugs in size, and no definite link with either culture was found at this stage. Of a sample of ten slugs dissected, however, the first two happened to contain perfect spermatophores in the spermatheca sacs. These were kept and labelled **A**.

Mating was first seen in July, among the young **R**, which produced a shorter spermatophore than **A**, with a hard collar attaching it at the entrance to the recipient's spermatheca duct. The offspring of the Wilmslow slug, mating in October and November, produced a spermatophore similar to **A**, found held in the recipient's spermatheca duct by a soft, sticky collar only.

Thus, by chance, cultures of **R** and **A** were already under observation when a big, rough, brown slug, which had to be labelled **B**, was discovered in quantity on tree-stumps in long wet grass at Buncrana, Co. Donegal, Ireland in August 1968. Eggs were obtained from these in November, which showed a red colour on hatching, and spermatophores of another distinct type were obtained from the brood mating in the following September. Grey slugs also found at Buncrana were later identified with **A**.

The problem of **B**, an Irish slug related to *A. hortensis*, yet easily distinguished from the ordinary grey form found in the same locality, showed the need for a clear definition of *A. hortensis*. The next attempt to examine the garden slugs at Sanderstead, by dissections in October 1968, yielded spermatophores of type **R** instead of **A**. This discovery initiated a programme of sampling from the same garden throughout the year, to determine the frequencies of the different types of spermatophore. In adults collected from November to March, yields were about 20%, the spermatophores quite clearly of two types **A** and **R**, with the proportion of **A** increasing steadily throughout the winter. Other details noticed in these garden samples, and compared with the cultures, gradually confirmed the suspicion that there were two different slugs living together without any sign of interbreeding.

The conclusion has been reached that **A**, **R** and **B** are a group of closely related species, hitherto confused under the name *Arion hortensis*. As the nomenclature is unsettled, they are still referred to throughout this paper as **A**, **R** and **B**. The purpose of this paper is to facilitate identification, and to stimulate further studies. Some comparative observations of *Arion intermedius* Normand have been added, as this is considered to be another closely related species.

PROCEDURE

This study developed unexpectedly, with no special equipment available, and with no premeditated plan. The slugs have usually been kept in unheated bedrooms, in assorted glass jars with more or less close-fitting metal lids. The jars are always furnished with moss and damp leaf-litter from a local oak wood, and other invertebrates included in this material have caused no trouble. The material provides lasting hygienic cover, and basic rations, which are supplemented irregularly, when time permits, with scraps of lettuce, chickweed, carrot, potato peelings, cucumber, or vegetable marrow, etc. During summer holidays all jars may be left unattended in a cellar for about three weeks, and most of the collection is also relegated to the cellar in warm weather, when a weekly inspection is usually possible. The advantage of glass jars in a bedroom is obvious when the light is switched on at night. The inhabitants are usually on show, on the lighter side of the jar, and activities such as courtship, copulation and egg-laying can be seen at a glance, and watched without disturbance. Conditions are neither constant nor natural, but extreme fluctuations are avoided. Except in the cellar, which is rather dark, the slugs probably always have plenty of light, as well as moisture, and sufficient cover for them to avoid excess.

These slugs are common enough to permit study by means of large numbers of quick dissections. They are prepared by a method that happened to be available at the outset, which has been retained because it can be used quickly and inoffensively at any time of day or night, even in a hotel bedroom, or in the field. A brief immersion in household methylated spirit effectively stills the slug, which is then opened immediately, while it is perfectly fresh and undistorted internally. A sample of 50 or so can be dealt with successively in this way very quickly after capture.

Since the discovery of the anatomical features of the three species, samples from different localities have been dissected, to check their diagnosis, to look for variations, and to record the different stages of the breeding cycle. The ovotestis is large, with a very lightly pigmented surface, in nearly mature and freshly mature individuals: the surface darkens as the organ shrinks and the pigment becomes concentrated, until it is very small and almost if not quite black in a senile animal.

COMPARATIVE STUDIES

a. *Size and general appearance* (Fig. 1). In the indoor cultures, individuals from a single batch of eggs, kept together, with the greatest possible equality of opportunity, have been found to

mature at widely different ages, from under six months to well over a year, and at sizes from about 2 cm, the smaller ones often doubling in size during later development, and changing considerably in general appearance. Some change in colour and shape is reversible, caused by stretching and shrinkage as eggs are produced and laid, and some change is permanent. Colour patterns tend to become blurred, black may fade to brown, and white may disappear or change to a dirty yellow. As the skin becomes more translucent, the neck shows the colour of the lower atrium, white at first, yellowing, and later perhaps a rusty brown, while the darkening and shrinking ovotestis may show through the animal's side, or dorsum, or footsole. The colour of the sole usually deepens, with an accumulation of orange or yellow granules, but these may be scarce, or sometimes almost white, particularly in some forms of **B**. Age may obscure the external differences between **A** and **R**, which were clear at hatching or at maturity.

After about four months of breeding, most of the slugs cease feeding, shrink and die more or less rapidly. Some degenerate rather sooner, and die still full of eggs, while others manage to survive as giants, reaching about 6 cm in **A** and **R**, and near 7 cm in **B**. The giants may live for another year or so, and die with or without shrinking first. A second breeding season has not been observed, but it could be a possibility in different circumstances, or at another stage of evolution. A pair of giant **A** separated during breeding, which continued from late March until early August 1970, showed some fairly normal mating behaviour when they were re-united in November. They also settled down as if to lay eggs, preparing a sticky patch on which no eggs arrived. Two odd eggs were found in the following February, but these did not hatch.

Similar variations and changes have been observed in *Arion intermedius*, with some individuals breeding at about 1.5 cm, and some growing to over 3.5 cm, still breeding.

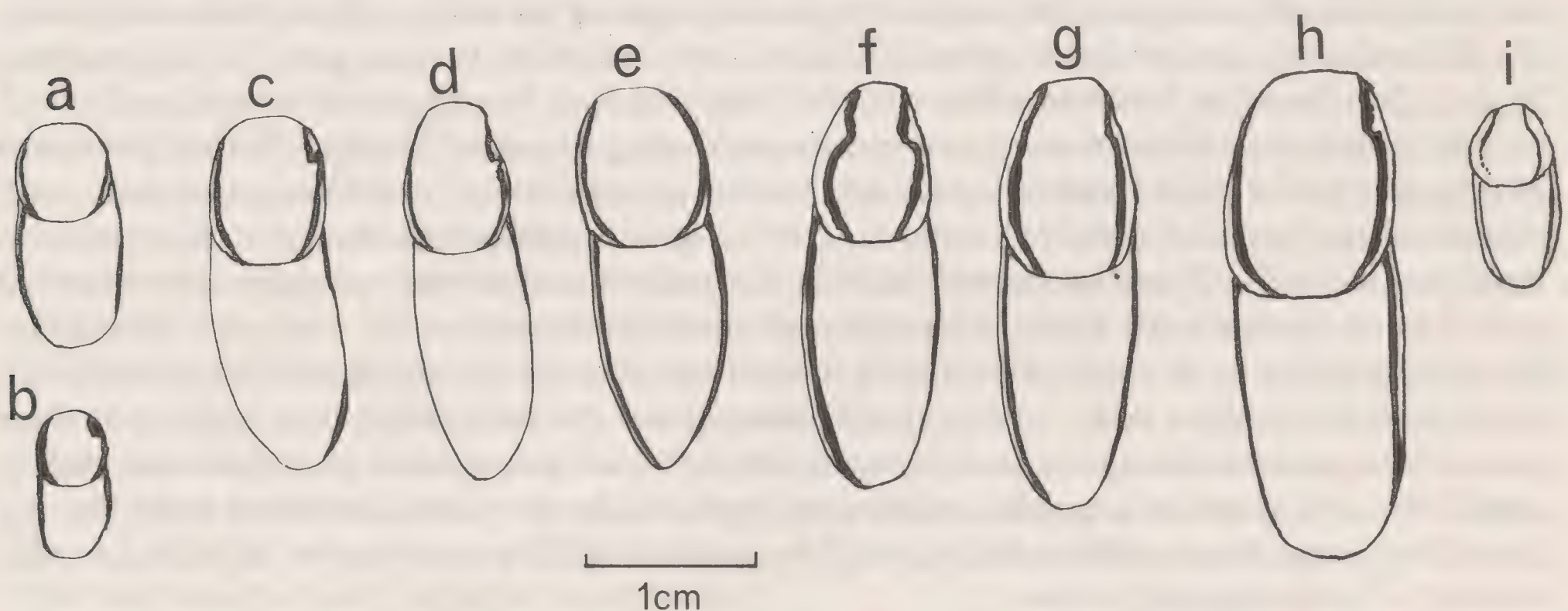


Fig. 1. Some typical shapes of the lateral pigmented bands as seen in animals at rest. a-b *Arion intermedius*; c-e form **A**; f-g form **R**; h-i form **B**.

b. *Colour*. The genus *Arion* evidently has a common stock of colour patterns and pigments, which are differently distributed in different groups and species, but with a tendency to parallel variation within these groups and species. Keys for identification, definitions of species, and many of their names, all refer to colour, and, in general, it is by their colours that they are known. Yet detailed surveys of the distribution of the different pigments are lacking.

The colours of a newly hatched slug can be comparatively easily defined, but the body pigments may become confused later, and the appearance modified by internal colour showing through unpigmented areas, as well as by colour in the dermal mucus. These additional factors are more subject to change with the animal's condition or diet, and have little taxonomic value. They do not affect the tentacles, and the red colour that so usefully distinguishes **R** from **A** is best seen in the clearer part of the tentacles.

The red colour tends to appear earlier than the other colours in young slugs, and to fade sooner in old animals. It is often practically confined to the tentacles, where it is easily recognized in juvenile **R**, and **B**, and has probably caused these to be confused with *A. subfuscus*. It has not been seen in **A**, or in *A. intermedius*, or in some less common forms of *A. subfuscus*. The various shades of brownish and violet tentacles seen in the former group may be classed together as derived from the same juvenile or embryonic red colour, and contrasted with the cold greys of the latter group. The same distinction between these two groups has been noticed when pigments are found on the internal organs, and, in particular, the integument of the fresh ovotestis, which, in the group with the coloured tentacles, may pass through shades of pink-brown or mauve, to a final dark brown or purple-black. Here again, the exact colour is not important, and in *A. subfuscus* a wide variation has been found in dissecting the offspring of a single slug.

The characteristic patterns of the genus are produced by the distribution of dark pigments, of which the most typical is blue-black in colour. This is the colour mentioned in the original description of *A. hortensis*, and it is the chief colour of both **A** and **R**. The presence of the same pigment in **B** is indicated by the blue-grey that is often apparent on the lower part of the animal's sides, even when the dark markings appear to consist of a brown variant. Brownish individuals of **A** and **R** have been seen to develop from blue-grey by ageing, or by contamination of the pigment with yellow or orange. The distinction between the blue-black and its brown variant is usually clear in juveniles, and again in spirit specimens, after the removal of the alcohol-soluble yellow and orange.

The red colour that is usually seen in the head and tentacles of **R** may be another variant of the blue-black. Occasionally it is well developed throughout the body, with or without the blue-black, producing the reddish slugs which have been noticed in various parts of England and Wales. One found in Pembrokeshire matched the Old Red Sandstone of its surroundings. A darker, rather chocolate-coloured, and more mature slug, found at Croydon, Surrey, produced 21 eggs, and two distinct kinds of hatchlings. Nineteen were of the typical blue-grey colour, with pinkish tentacles, and the other two had exactly the same banding pattern, but in pure red, with matching tentacles. These two were mated in due course, and all their progeny were pure red also. Mixed broods with blue-grey majorities were produced by the rest, and subsequent breeding resulted in no new colour, but in further variation in the amounts of the two colours. Some individuals show both colours clearly throughout the body at an early stage, but these cannot be separated absolutely from those in which the red is restricted to the anterior end, as small amounts of red are quickly masked or replaced by grey. Adults raised from the red hatchlings range from reddish-black through brownish and dirty mauve-grey, all with a certain amount of superimposed yellow.

The two species, **A** and **R**, which have been confused for so long, both show much variation in the amounts of orange or yellow, and of the dark pigment, and also in the width and clarity of the darkly pigmented bands. Differences which are not general distinctions may, however, be used to distinguish the species in any one locality. For example, an English garden may have adult **A** in which the black and grey pattern is so overlaid with orange or yellow as to appear completely brown, or dirty yellow in the palest individuals, the sides are nearly always darker than the dorsum, and white appears only in the lowest row of tubercles of some individuals. The typical forms of **R** in the same garden will stand out as darker, or more black and white animals, with white appearing usually in considerable amounts on the sides, restricted to the lowest row of tubercles only in the darkest individuals. Descriptions and illustrations of these colours may suggest identification of the species, especially when two forms are compared, but only very doubtfully, unless there is also a clear indication of the internal tentacle colour underlying any black, or a definite statement of a distinctive position and shape of the upper edges of the mantle bands, which in **R** are higher and closer, with a more longitudinal direction posteriorly, and in **A** are lower, often with a deep notch or even a break over the respiratory pore, and more

convergent posteriorly. Some of the more characteristic forms of the bands are sketched in Fig. 1, from animals in their natural resting positions. In this position, which is easily seen in the field, **R** (Fig. 1f–g), can often be quickly distinguished from **A** (Fig. 1c–d). The bands in **B** (Fig. 1h–i), tend to resemble **R** rather than **A**, and in *A. intermedius* (Fig. 1a–b), they tend to resemble **A**.

c. *Spermatophores* (Fig. 2). If these slugs are confusing in their external appearance, they are easily defined by their spermatophores (Fig. 2). **A**, **R** and **B** have spermatophores differing from those of other species of *Arion* in being shorter, and in having the posterior end bent, or curved in the form of a hook. There could be a similar form in *A. intermedius*, but in this species copulation has never been observed, and when the appearance of a spermatophore has been seen in the spermatheca it has always disintegrated and has not been successfully unfolded.

As **A**, **R** and **B** are all gregarious, and mate freely, it is not difficult to obtain spermatophores by dissection of freshly collected adults. The first 12 months of sampling from the mixed garden population yielded spermatophores of **A** from November to June, with a maximum in February and March, and spermatophores of **R** from September to March, with a maximum in October and November. The spermatophores, even when incomplete, can be identified without hesitation, although some variation in size and detail, within clearly defined specific limits, is as noticeable as the variation of the slugs themselves. Pairs of exchanged spermatophores, however, and indeed pairs of copulating slugs, are remarkably well matched. If the slugs are mating repeatedly during continued growth and development, they would appear to be selecting partners at a similar stage. The first direct observation of the same pair mating twice was made by chance with captive **B**, on 10 October and 22 November 1969. Both had deposited their first clusters of eggs shortly before the second occasion. With a pair of **R**, an unsuccessful attempt at mating was observed on 9 September 1972, and a completed mating on the following evening. One of them was seen laying eggs on 27 September, and the pair mated again on 28 September. Matings unobserved and in natural conditions are likely to be far more frequent.

To obtain a series of spermatophores from the same individual, one of the 'red' colour variety of **R** was used. At the first mating, on 13 September 1971, the partners were about seven months old, and subsequent matings of the red individual with ordinary grey slugs took place on 18 October, 2 and 12 November and 2 December. The experiment was limited, not by the slugs, but by lack of time for observation, and it has not been repeated for the same reason. On each occasion when a slug of similar age was introduced, courtship began within an hour or so, and copulation followed fairly quickly on two occasions, but on two other occasions not until the same partner was re-introduced a day or two later. The red slug laid its first eggs on 25 October, a week after its second mating. The five spermatophores did not differ significantly, except that the first was distinctly smaller than the rest.

Fig. 2 shows the important features of the spermatophores. The *nozzle* (n in Fig. 2), which is the softest and most flexible part, is deflected through about 90° in **R** (Fig. 2d–f), and more forward-pointing or slightly bent in **A** (Fig. 2a–c) and **B** (Fig. 2g–i). The *longitudinal ridge* (lr in Fig. 2) is more or less strongly serrated in **R** and **B**: in **R** (Fig. 2e–f) it may turn, posteriorly, away from the convex side of the hook, through not more than 90°, while in **B** (Fig. 2g–i) it spirals through 450° about the axis of the spermatophore. In **A** (Fig. 2a–c) the ridge may easily be overlooked in some specimens: it is never strongly serrated, but is low and inconspicuous, keeping to the same side of the spermatophore throughout its length. The *posterior hook* (ph in Fig. 2) is very definite in **R** (Fig. 2e–f), and usually rather less so in **A** (Fig. 2a–b) and **B** (Fig. 2g–h). On one occasion only, a pair of **B**, disturbed by accident just before coitus was completed, received spermatophores with rather narrow, straight tails (Fig. 2i), which remained projecting as they were too long to enter the atrium. Both were removed by dissection.

d. *Transference of spermatophores* (Figs 3 & 4). An important feature of these three species (and *A. intermedius*) is the very short spermatheca duct. This is quite inadequate to hold the wide portion

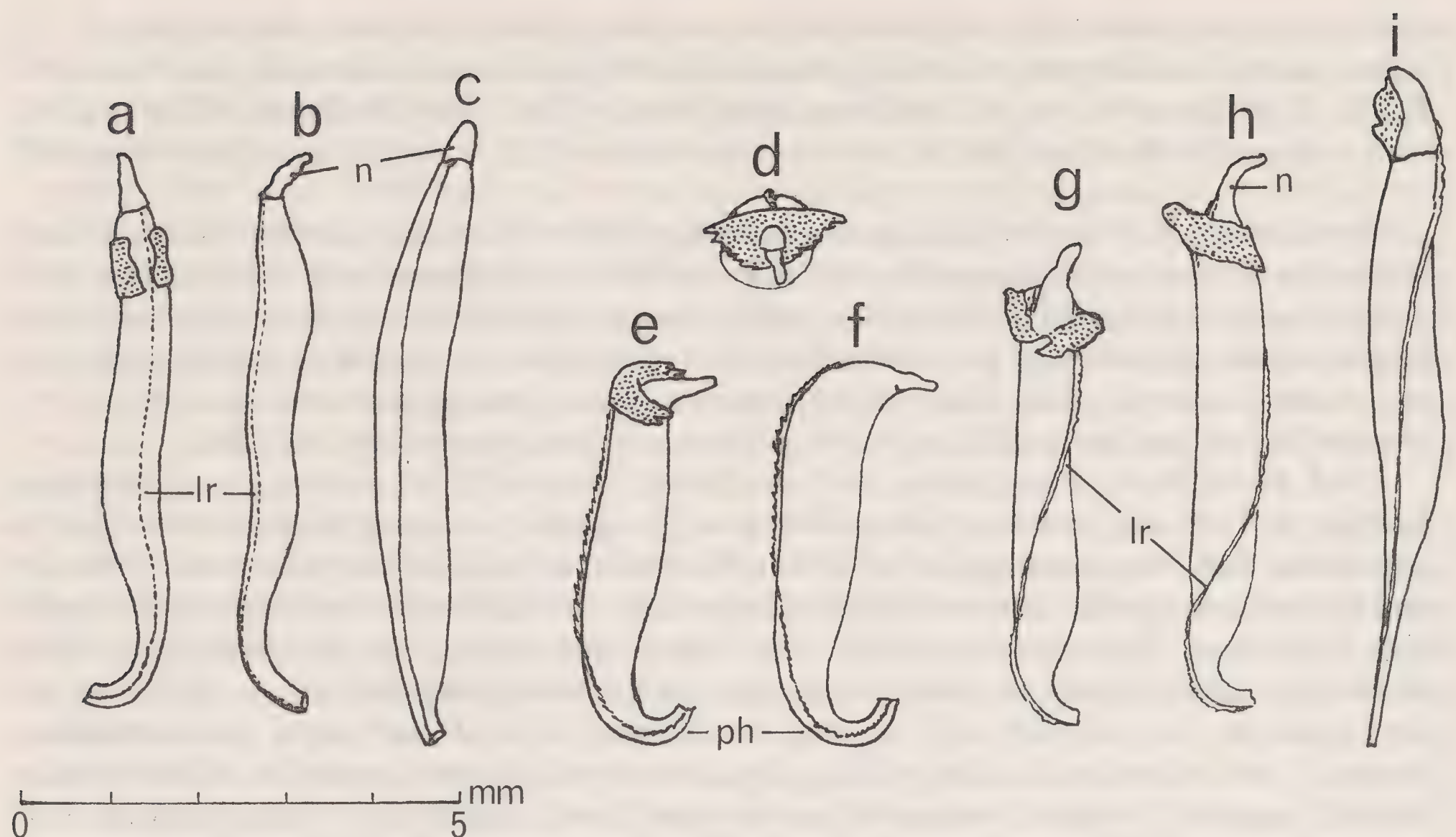


Fig. 2. Spermatophores. a-c form **A**; d-f form **R** (d anterior view); g-i form **B** (i an atypical example with a long tail). Attachment collars stippled, lr longitudinal ridge, n nozzle, ph posterior hook.

of the spermatophore, to grip it and to draw it away from the donor, as does the longer duct of *A. subfuscus*. Not surprisingly, it is found that the three species with distinctive spermatophores also have distinctive mechanisms for their transference. A good grip is particularly necessary to obtain from the donor a spermatophore with a hooked tail. The differences in the structures concerned evidently constitute a physical barrier to interbreeding, as well as providing excellent diagnostic characters for the three species.

A recently transferred spermatophore can only be detached from the recipient with some difficulty, and in each species it comes away with some kind of additional structure, which may be described as a collar (stippled in Fig. 2). In **A** (Fig. 2a) the collar is comparatively short-lived and indistinct. It may be little more than a sticky patch by which the spermatophore adheres to the receiving area at the entrance to the recipient's spermatheca duct, which is thickened. In **R** (Fig. 2d-e) and **B** (Fig. 2g-i) the receiving areas are around rather than within the entrance to the spermatheca duct, and the collars are hard projections, which come away with jagged edges. By the entrance to the duct in **B** (Fig. 4e-f) is a variable amount of firm thickening, not unlike that in **A** (Fig. 4a-b), and there is also a conspicuous white conical knob, which can be seen lying uppermost during coitus (Fig. 4e-f and Fig. 6c). In a dissection of **R**, the spermatheca duct may appear to be thickened, but the apparent thickening within the duct is a soft flap which unfolds into the atrium to form a receptive area. Quick (1946) gave an account of the spermatophore and its attachment in **R**, but, failing to distinguish any nozzle, he described the collar as being a flattened anterior end of the spermatophore.

The actual formation of the attachment collars cannot be seen, but each species has a characteristic structure associated with the termination of the epiphallus, in a suitable position to precede the spermatophore and prepare the collar on the receptive area. Figs 4 and 5 indicate the form and position of these structures which are marked e. In **A** (Fig. 5a-b) it is a rather stiff plate folded round the termination of the epiphallus to form a conical lid. (A similar, but lower, conical lid has been seen in *A. intermedius*.) In **R** (Fig. 5c) a similarly stiff plate stands up as a barrier between the epiphallus and the spermatheca duct, where it could be pressed round a

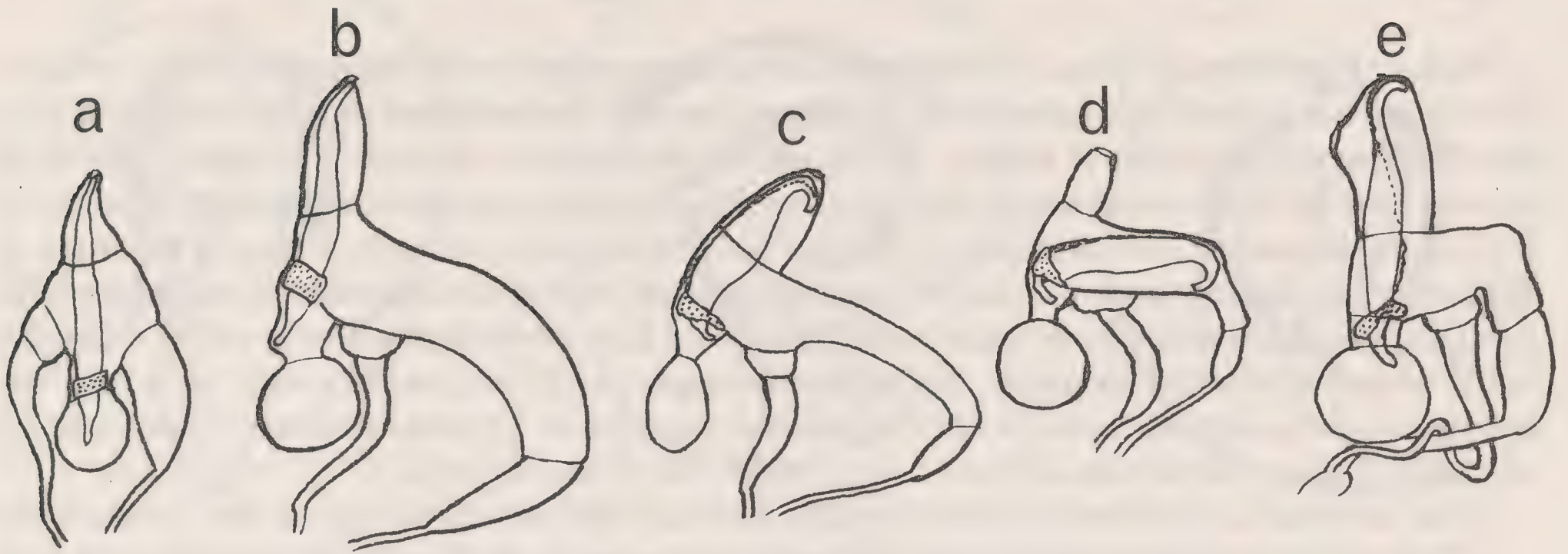


Fig. 3. The distension of the atrium by a spermatophore. The attachment shown stippled and the outline of the spermatophore completed after further dissection. a-b form **A**; c-d form **R**; e form **B**.

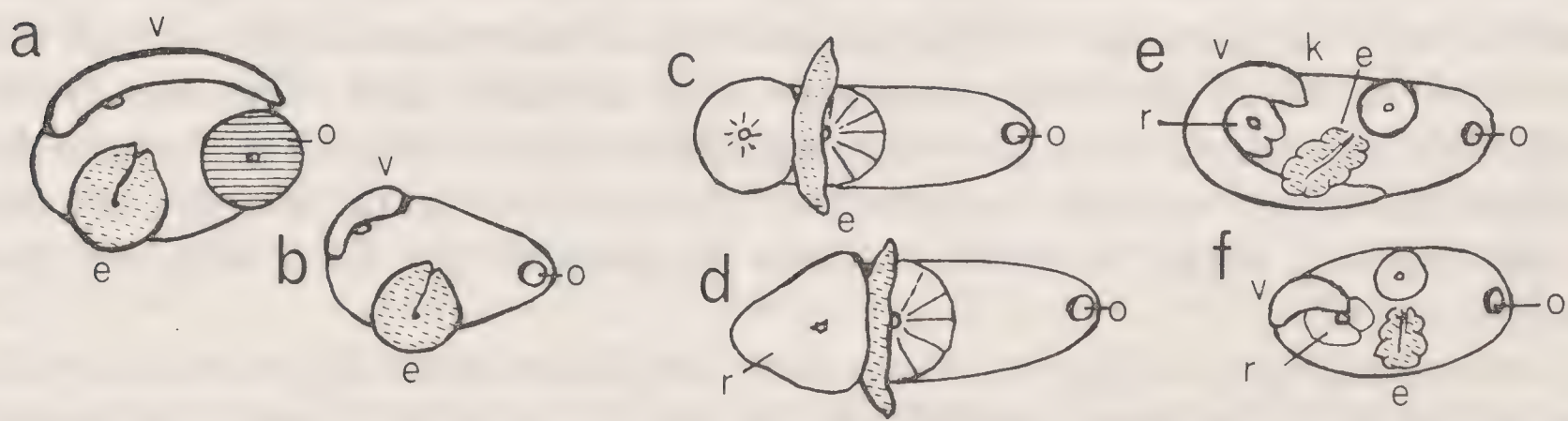


Fig. 4. Plan of structures seen within the atrium. a-b form **A**; c-d form **R**; e-f form **B**. e distinctive structure associated with the epiphallus, k conical white knob in form **B**, o opening of oviduct, r receptive surface in forms **R** and **B** (not seen in Fig. 4c because it is tucked into the spermatheca duct), v variable thickening around spermatheca duct in forms **A** and **B**.

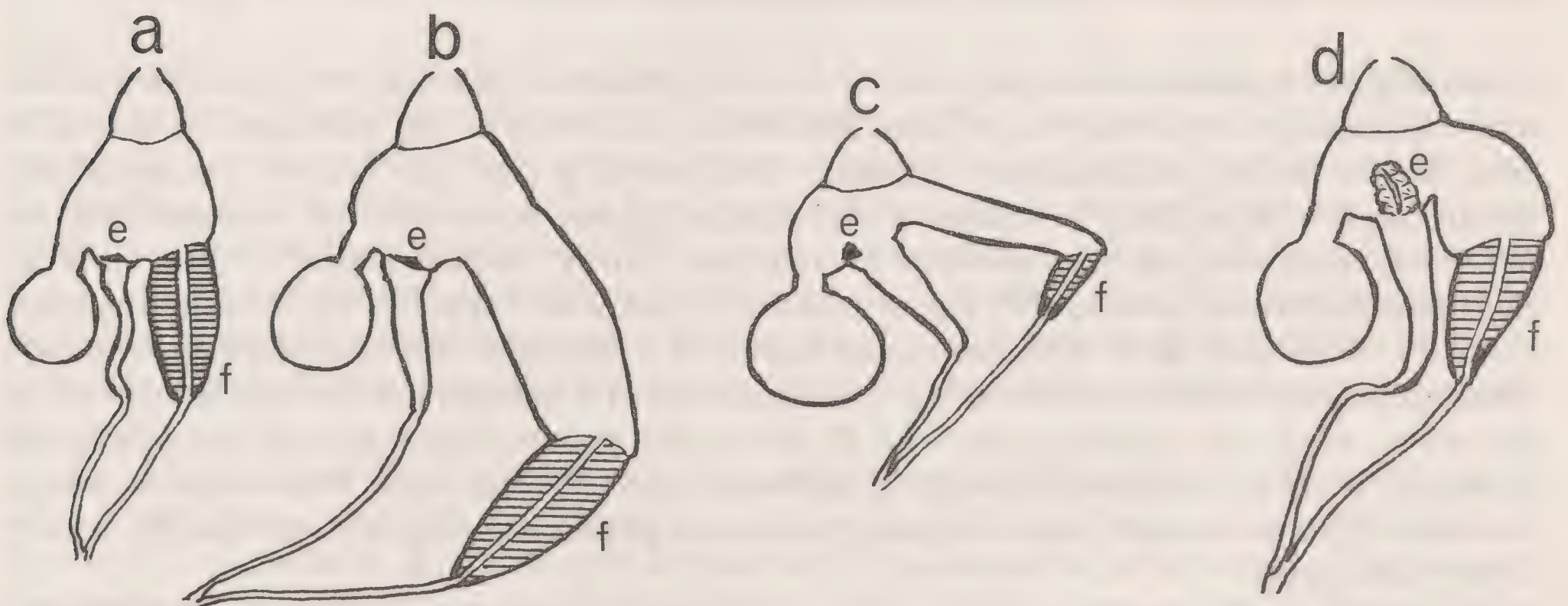


Fig. 5. Proportions of the regions of the oviduct. a-b form **A**; c form **R**; d form **B**. e characteristic structure associated with the epiphallus, f firm portion of the oviduct.

spermatophore to fit on the partner's receiving area. In **B** (Fig. 5d) there is a softer structure, with a crenate outline, and usually with some pink or purple pigmentation.

e. *Oviduct* (Figs 5 and 6). These three species show interesting developments of the free oviduct (which are not shared by *A. intermedius*). A rather long narrow proximal portion is followed by a firm thick-walled portion (f in Fig. 5), on which the retractor muscle is inserted. The firm portion may be thrust out during coitus, to an extent depending on the development, distally, of a dilated thin-walled eversible region, which could be regarded as an extension of the atrium. This eversible region contains a double longitudinal fold ending in the atrium, comparable with the ligula of other species. It does not however expand into a wrinkled adhesive surface, like the ligula of *A. subfuscus* for example, but it has the aspect and function of a sole, on which the emerging oviducal process creeps with a snail-like movement. Its form becomes clearer when it has picked up a yellow colour from contact with the dermal mucus.

The differences between the three species here are differences of degree and proportion.

The greatest variation in the eversible region is found in **A** (Figs 5a–b), which tends to a clear dimorphism, with few intermediates, between the minimum and maximum development. The alternative conditions, which can be distinguished quite early in development, and are never successive stages, are inherited. Both kinds of individual have often been noticed among slugs raised from the same cluster of eggs, while broods of at least 30 in each case have been found by dissection to be all alike when raised from a pair of like parents. Of the first 10 matings observed in this species, there were two in which both partners had the large eversion, six in which one had and the other had not (Fig. 6a), and two in which neither partner had. Neither of the two conditions is at all obviously advantageous or necessary, and either may predominate temporarily in a population. Both have been found however in every locality where they have been studied, including a sample from Halifax, Nova Scotia. On the average, the form with little or no eversible region is about twice as frequent as the form with the maximum development.

The eversible region in **R** (Fig. 5c) is invariably long and narrow, and more than sufficiently developed to cover the firm portion of the oviduct, which is relatively small. The everted organ is finger-like, and more mobile than the bulky structure in **A**, but it is not very often seen fully extruded. It may be withdrawn several times during coitus, and is often only partly extruded. It may be tucked underneath the animals, or it may play over the partner's back (Fig. 6b).

The oviduct of **B** (Fig. 5d) resembles that of an intermediate form of **A**, with a very moderate development of the eversible region, sufficient to allow the rather bulky firm portion of the oviduct to be extruded as a short, immobile process (Fig. 6c).

f. *Courtship and copulation*. Courtship may be brief or protracted, and may be abandoned at any stage. A sexually active slug may follow, and nibble, members of the other species, and of its own, before finding a satisfactory partner. Even when a pair has become encircled and apparently settled, with the genital atria beginning to appear, coitus does not necessarily follow. However, when the genitalia are fully everted and joined, there is almost certain to be an exchange of spermatophores, after a predictable interval, which depends on the species. **A** takes about 20–30 minutes, **B** 30–60 minutes, and **R** 80–105 minutes, or sometimes longer. Probably, the shortest time is needed to attach the spermatophore of **A** because it is the least firmly held of the three, while the spermatophore of **R** needs the firmest attachment to overcome the resistance of the strong forward-pointing serrations and posterior hook. Differences in timing and differences in structure may be equally effective in preventing success if interspecific mating is ever attempted.

When the hook is finally jerked away from the donor, there is enough force to dislodge the spermatophore from its collar also, if this has not been adequately secured, or if the movements of the separating animals give it an unfortunate twist. This was seen to happen at the end of an

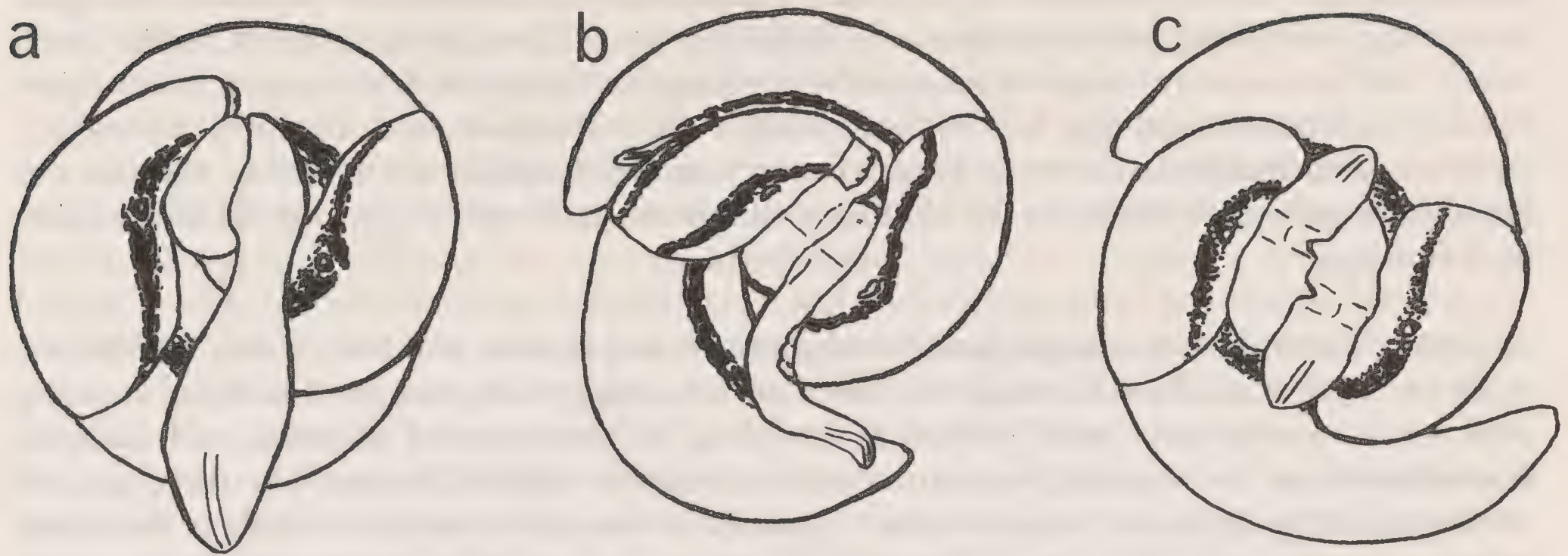


Fig. 6. The oviduct everted in coitus. a form **A**; b form **R**, c form **B**.

otherwise normal mating of **A**, when one partner, having just obtained a spermatophore, hurried away so quickly and at such an angle, across the other slug, that the second spermatophore came adrift between the two, and was lost. Discarded, collarless, spermatophores, possibly resulting from similar mishaps, have been found occasionally in cultures of **R**, and of **B**. Once, a spermatophore of **R** was found when an individual of this species was kept with one of **B**, suggesting that they may have attempted to mate. Both survived for some time, and produced only a few infertile eggs, as unmated slugs often do. However, apart from one occasion when **A** and **B** were seen briefly encircled, nothing beyond a slight preliminary courtship or investigation has been observed between the different species. Breeding has only occurred when a slug has had a mate of its own species. In this, all three differ from *A. intermedius*, which breeds unmated.

Apart from the different times of duration of coitus, and the different forms of everted oviduct, which are sketched in Fig. 6, the mating process is very similar in the three species. Other details vary within the species, especially the degree of external activity. The slugs may remain practically motionless until they are almost ready to separate, or there may be intermittent circling movements, which sometimes add up to several complete clockwise rotations of the pair. Some slugs, especially **R** indulge in a good deal of licking, or nibbling, not only of their partner, but also of their own everted oviduct.

g. Reproductive potential. The three species all breed freely in captivity, usually with a very high rate of fertility. The normal productivity of an average slug, however, is not easily assessed, because of the range of individual performances. Some fail to breed at all, and in a group with low production it is difficult to judge how many are actually breeding. Of the few individual totals recorded, the highest have been: 310 eggs in 11 clusters, and 277 in 10 clusters, for a pair of **A**, separated when the first eggs were laid; 281 in 12 clusters, and 237 in 10 clusters, for a pair of **R**; 367 in 16 clusters shared by a pair of **B** kept together. All these took about four months to complete their tallies. An exceptional individual of *A. intermedius* took six months to produce 302 eggs in 19 clusters.

The highest numbers of eggs counted in a single cluster are 68 for **A**, 56 for **R**, and 39 for **B**, all in first clusters, and 27 for *A. intermedius*, in a mid-season cluster. Numbers between 10 and 30 are more frequent in **A**, **R** and **B**, and as many as 20 is unusual in *A. intermedius*. The size and toughness of the eggs usually increases slightly as the number decreases. In **A**, **R** and **B**, the number of eggs in a cluster is often equal, or very nearly equal, to the number of days since the previous cluster was laid, and the mean daily rate of approximately one is maintained

throughout the breeding season. Individuals of **A** and **R** which sometimes have twice as high a rate of egg production maintain their own individual rate. These observations of steady rates, unaffected by seasonal change in four months, suggests that adverse conditions which only delay the actual deposition of eggs will not necessarily reduce the final total. In the *A. intermedius*, which with its smaller and more frequent clusters is an easier subject for this study, the rate was found to drop from about two in the autumn to about one in the winter, picking up to two again by February.

h. *Breeding season.* The breeding seasons of slugs are often extensive, and tend to defy satisfactory study and definition. As individuals can breed at such steady rates over periods of four months, there need not be any 'peak' period of breeding in these species of *Arion*, and seasonal fluctuations may be irregular, and attributable to various external factors. The three species, when occupying the same territory, and apparently favouring the same kinds of food and external conditions, might be expected to fluctuate in unison, but it has been observed throughout that each tends to predominate, and to breed, in a different part of the year. An attempt must therefore be made to describe their separate seasons. A fuller study of the differences would probably do much to explain the distribution patterns of the species, and their pest-ratings in agriculture and horticulture. Adequately sheltered eggs and juveniles appear to survive long periods of inactivity in adverse weather conditions, when the adults nearly all succumb. At low temperatures, the eggs take 10 weeks or more to hatch, whereas in summer they hatch in three or four weeks.

Direct observation of hatchlings and young slugs is dependent on weather conditions, and quantitative sampling of total populations is not practicable in the situations where the slugs abound. In a garden, eggs and young are likely to remain hidden in inaccessible underground shelters. Systematic collection of slugs from the surface, and from under plants, flat stones and boards, has been used to gain an idea of the main seasons of abundance of freshly mature, mating, breeding, and senile individuals, of each species. Some rule is necessary to decide which slugs should be counted as breeding at the date of capture, and it is convenient to assume that the mean daily rate of egg production may be taken as unity, and that a breeding individual therefore is one which will produce any number of eggs within that same number of days. This defines the breeding period as beginning some time before the first eggs are deposited, perhaps 30 days, since first clusters often contain about 30 eggs. The breeding period ends, and senility begins, when egg production ceases, or the rate suddenly drops with the production of a few eggs which are usually abnormally large, and infertile.

These slugs are basically annual. Captive **B** from Buncrana have kept an annual cycle for more than eight years, in which matings have been frequently observed during the months September–January, and breeding has been heavy in November–February, only rarely extending beyond the limits of October–March. In late August and early September, when visits have been made, in different years, to Buncrana, Fowey and Highgate, **B** has been found mainly about half-grown to full-grown, with freshly mature and nearly mature, as well as immature, individuals. In late October, at Fowey and at Swansea, **B** was clearly at an early stage of the breeding season, with many still not quite mature, and none senile. Out of season, this species is inconspicuous, and only a few senile and juvenile animals have been found in April, at Highgate. Thus in **B** at least, the natural breeding season appears to be about the same as that observed in the cultures. Breeding out of season has not been seen in the field, but **B** of Fowey and of Highgate stock, from the earliest broods hatched in captivity in October 1971, matured to breed in early April 1972. Some of the Swansea stock also, which hatched in December, were breeding in mid-June 1972. These spring and summer breeding slugs died quickly, and did not have a long successful season as in the winter.

Breeding within six months of hatching, which appears to be unusual in **B**, is much more frequent in captive **A** and **R**. Many individuals take 9–11 months, or longer, and some fail to

breed at all. The overall result is an annual repetition of the heaviest breeding, together with a rapid spread of the breeding season, as the brood of a single slug can produce a continuous supply of eggs until well after the next generation has taken over.

General observation in the garden has suggested that both **A** and **R** cease to breed in a hot dry summer, when adults die quickly, and juvenile development is retarded, as happens in cultures also. **R**, which is scarce after a severe winter, but breeds well into the spring after a mild winter, disappears before **A** as summer approaches, and also reappears before **A**, being conspicuous as juveniles feeding on fallen fruit, and maturing during the autumn. Most **A** are less mature than the **R** in autumn, and not ready to breed until the later part of the winter, or the spring. The breeding season of **A** may therefore be said to follow that of **R**, after some weeks or months. **A** is also rather less sensitive to extreme conditions of winter or summer, and its season has a greater tendency to extend to 12 months. An ending or decline of the breeding season is particularly difficult to observe in **A**, as freshly mature adults continue to appear until perhaps a summer drought makes it difficult to find any slugs at all.

The same sequence in their main season of maturity, **B** followed by **R**, followed by **A**, has been apparent wherever the three species have been found on the same ground. Where **A** occurs alone, its season may be less obvious, but very high proportions of freshly mature individuals in early November samples from Wilmslow, Cheshire, and from Halifax, Nova Scotia, suggest that winter is the main breeding season. Summer-breeding, however, may be more important and necessary in districts where the growing season is short, and **A** probably adapts to such conditions more readily than **R** or **B**. **A** appears to be the most widely distributed of the three species, especially in the north. In Scotland, adults have been found in the summer, but no observations have been made in the winter.

Slugs may remain active through frosty weather in suitable shelter, often within living or decaying plant material underground. Here, winter conditions hinder observation, rather than hindering the slugs, and their effects are not immediately seen. Autumn breeding appears to be delayed after a long summer, possibly because a fall in temperature is needed for the new season's slugs to begin mating. In 1969, an impressive outburst of mating was observed in all jars of **B**, on the first chilly September night after a hot summer. In winter, mating takes place at any time of the day, indoors or outside. **A** has been found mating under stones when snow lay on the ground.

i. *Distribution*. Three species which flourish and breed at different seasons in the same place will be differently affected by the same climate. All three, however, appear to be favoured by a long growing season, and are probably restricted as much by the duration as by the severity of hard weather in winter, or drought in summer. **A**, **R** and **B** in fact show differences as well as similarities in their distribution patterns.

A, the species with the longest and least definite season in favourable conditions, is the most tolerant, and it may occur in all parts of the British Isles. It has been recorded alone, without **R** or **B**, in parts of Ireland, and of Scotland, and northern and eastern England. In southern England it is usually found alone only in places where it is not particularly abundant.

R is found abundantly, and more or less closely accompanied by **A**, in southern England and Wales, from Kent to Cornwall and Pembrokeshire, and rather less generally in central and northern England. Apart from a single slug taken near Belfast, **R** has not yet been found in Ireland.

B is obviously at home in Inishowen, E. Donegal, where it is much more widespread than **A**, and, near Buncrana, it has been found in many kinds of habitat—marshy river-bank, garden, farmyard, field and roadside, right up into the hills in the pathside grass, surrounded by open moor and bog. In the rest of Ireland it may be more local. It has been found in a number of localities in southern Scotland. In England and Wales it seems to be more or less restricted to certain rich and well sheltered spots, which support all three species, such as Highgate

Cemetery in London, a disused chalk quarry at Boxford, Berkshire, and some roadsides near Swansea, Glamorgan. In Cornwall, however, further investigation has shown its presence in a wider area around Fowey, and not only in Covington Woods which at first appeared to be its only home.

Both **A** and **R** appear to be widespread in France, but little is known of the species in the rest of Europe. From North America one sample only has been seen, of **A** alone, from Halifax, Nova Scotia.

A. intermedius, like **A**, is found in all parts of the British Isles, but its distribution pattern is independent. It may occur with the three species, or with none of them.

SUMMARY DESCRIPTIONS

The differences between the three species are summarized in the illustrations, and in the following brief accounts. External appearance may be distinctive, but is variable and can be misleading, and identification should be checked by anatomy and spermatophores.

a. *Species A*. Adults usually measure 2–4 cm extended, sometimes reaching 6 cm in captivity. The body is usually rather smooth and cylindrical. Typical pigmentation is blue-black, in variable quantity, usually well sprinkled with yellow. True brown and red, as opposed to effects of black plus orange in senile slugs, have not been seen with any certainty. Any pigmentation on the epiphallus, and on the ovotestis, is black or grey. The transparent bases of the tentacles show only a cold or greenish grey. The dark lateral bands are rather low on the body, and may be narrow, but very often the dark pigmentation continues down almost to the foot-fringe. The upper edge of the right mantle band often dips deeply, or breaks, over the respiratory orifice (Fig. 1c, d).

Adults are conspicuous in winter and spring, the main season following that of **R** where the two species occur together. **A** also matures throughout the year, and may be found in any part of the British Isles.

The spermatophore measures about 5–7.5 mm, and is rather straight, or slightly sinuous, with a more or less forward-pointing nozzle, and the posterior end hooked to a variable degree (Fig. 2a–c). A low and often inconspicuous ridge, which is never strongly serrated, keeps to the more convex side of the spermatophore. A soft, sticky collar holds the head of the spermatophore (Figs 2a and 3a, b) within the entrance to the recipient's spermatheca duct, through which the spermatophore passes when, after discharging through its tail into the atrium and oviduct, it is sufficiently deflated to fold completely into the spermatheca sac. Spermatophores found by chance in dissecting are nearly always in a distended spermatheca sac.

The most reliable character of **A**, apart from the spermatophore, is the flap covering the termination of the epiphallus within the atrium (Figs 4a–b, 5a–b). This detail resembles *A. intermedius* rather than the other two species **B** and **R**.

The firm portion of the free oviduct is very well developed, and may almost fill a very large thin-walled region which is everted with the atrium in coitus (Figs 5b, 6a). More often, however, the eversible region is not developed (Fig. 5a). Both forms occur in all localities, and appear to mate indiscriminately.

The duration of actual coitus, under observation, has always been between 20 and 30 minutes.

b. *Species R*. Size and texture are very similar to **A**, but large animals sometimes appear to be slightly rougher. As in **A**, the typical pigment is blue-black, but this may be accompanied, preceded, or even replaced, by red. A tinge of red can usually be seen in the tentacles, especially in juveniles, and the red often shows clearly in the eggs just before hatching. Any pigmentation on internal organs may include red, and the ovotestis is often brownish or mauve-grey. As in **A**,

the whole body may be dominated by black, or by grey mixed with yellow and orange, but the more typical **R** is rather more distinctly banded, with black and white. The mantle bands (Fig. 1f–g) are usually somewhat higher and closer than in **A**, arching over the respiratory orifice, which may be in a whitish region. The animal's sides, below the lateral bands, are often white, with darker grooves.

Adults are conspicuous in autumn and winter, rather earlier than the main season of **A**, which tends to replace **R** gradually during the winter months. **R** is widespread and abundant, together with **A**, in southern England and Wales, in some districts farther north, and probably in most of France.

The spermatophore (Fig. 2d–f) is about 4–5 mm, and relatively much wider than in **A**. The nozzle is deflected through about 90°, and the posterior end strongly hooked. A strongly serrated longitudinal ridge turns, posteriorly, through not more than 90° about the axis of the spermatophore. A hard collar attaches the head of the spermatophore to a soft flap at the entrance to the recipient's spermatheca duct (Figs 2d–e, 3c–d). The spermatophore remains for perhaps about 18 hours thus fixed in the atrium, where it is usually found. Only the anterior end, broken at the collar, is at all commonly found in the spermatheca sac.

The most distinctive anatomical feature of **R** is a conspicuous, rather stiff flap, about 1 mm long, projecting between the terminations of the epiphallus and the spermatheca duct in the atrium (Figs 4c–d, 5c).

The firm portion of the free oviduct is less bulky than in the other two species, and is easily covered by a long, narrow eversible region, constituting a mobile, finger-like process (Figs 5c, 6b).

Actual coitus has been observed to last for at least 80 minutes on many occasions, and for 90–105 minutes on some. One pair, found in the garden in January, remained with conjoined atria for over three hours.

c. *Species B*. Adults measure about 2–4 cm, the range as in **A** and **R**, but the average slug appears to be larger than the other species. The tubercles are coarser, even, and rather sharply ridged, or angled, giving the appearance of a very regularly chiselled surface. The black or dark brown pigment is very variable in quantity, and is usually concentrated in dots or stippling, on a light brown or yellowish background. Typically, it is a brown slug, with distinct bands, and greyish sides. The mantle bands are usually rather high over the respiratory orifice, and close anteriorly, as in **R**, but they may be broken, or represented by a few dots only. The eggs are usually quite pink before hatching, and the young a reddish brown. Red or violet is usually apparent in the tentacles, and in any pigmentation on internal organs.

B usually matures from September onward, slightly earlier than the main season for **R**, and breeds through autumn and winter. Its season is better defined, and its distribution more restricted, as compared with the other two species in the British Isles. It is one of the commonest slugs in Inishowen, Co. Donegal, and is locally common in some mainly western parts of southern Scotland, England and Wales.

In the size and general form of spermatophore, **B** is intermediate between **A** and **R**, although in one exceptional case the tail was drawn out to bring the total length of the spermatophore to 7.5 mm (Fig. 2i). A conspicuous and more or less strongly serrated ridge spirals through 450° about the axis of the spermatophore, and a corresponding spiral line is clearly seen on the epiphallus in a fresh dissection. A hard collar, as in **R**, attaches the head of the spermatophore to the thickened lip of the spermatheca duct in the recipient (Figs 2g–i, 3e). Later, the spermatophore passes, collarless, through the duct, and may be found folded in half in a distended spermatheca sac.

The distinctive feature in the atrium is a crenate structure associated with the termination of the epiphallus (Figs 4e–f, 5d). It often carries pink or purple pigment.

The firm portion of the free oviduct has very thick walls, with four inner strands giving the

lumen a cruciform section when contracted or fixed. The eversible region, with the atrium, is barely sufficient to cover it, so it lacks mobility when extruded (Figs 5d, 6c).

The duration of actual coitus, under observation, has always been between 30 and 60 minutes, another detail in which **B** appears intermediate between **A** and **R**.

ARION INTERMEDIUS

Comparisons between *A. intermedius* and the *hortensis* group have been noted repeatedly, both in field encounters and in cultures. *A. intermedius* gives the same general impression of the group, probably coming closest to **A**, but often superficially resembling juvenile **B**.

In captivity, the soles are frequently observed on the sides of glass jars, and it is certain that the species cannot be identified by their soles. **B** and *A. intermedius* often match exactly, with pale or golden-yellow soles, and are sometimes matched by **A** and **R** too. **A** and **R** more frequently, and **B** and *A. intermedius* occasionally, attain a deeper orange. The rough tubercles of juvenile **B** and of *A. intermedius* can be confused at first sight, although their ridges are rather smoothly continuous in **B** and broken in *A. intermedius*. In the same two species, the pigmented bands share a tendency to appear stippled, and are sometimes much reduced, or absent.

In the typical position, and in the quality, of the dark pigment, *A. intermedius* resembles **A**, with a blue-black pigment, and cold grey tentacles, and without the characteristic brown of **B**, or the red of **B** and **R**.

A. intermedius is generally much smaller than the other species, but adults vary from about 15 mm to well within the range of the *hortensis* group, and giants often develop in captivity. The eggs may be indistinguishable, as the ranges of intra-specific variation overlap considerably. Typically, however, the eggs of *A. intermedius* are slightly smaller, and have more opaque white in the surface layers. Relative to the size of the slug, they are slightly larger, and they are deposited in smaller clusters, often of less than 10 eggs, or even singly.

The most significant anatomical resemblance is in the very short spermatheca duct, which would suggest a short, *hortensis*-like spermatophore in *A. intermedius*. The termination of the epiphallus in *A. intermedius* has a structure closely resembling that in **A**, where it appears to be associated with the production of the sticky collar. However, no mating has been recorded, and no spermatophore is known in *A. intermedius*. The spermatheca sac may be found filled as in **A**, but anything resembling the form of a spermatophore disintegrates on touch. The oviduct is short, and lacks any specialization associated with the mating process, and it may be that the process has been abandoned in *A. intermedius*, or at least in its common British form. There could be problems with the apparatus, because, if the mating process were as in **A**, but briefer, omitting any activity of an everted oviduct, the collar could be less secure, and the risk of losing spermatophores between animals on separating after coitus would be high.

In captivity, *A. intermedius* has certainly bred without mating, and its breeding seasons are even more irregular than in **A**. Many individuals fail to breed, some begin to breed at more than a year old, and others have begun at less than three months. Three life cycles have been completed in one year.

On the whole, *A. intermedius* seems to be a winter slug, or perhaps a more northern species than the others. The tendency of the group to aestivate in captivity is most marked in *A. intermedius*. In warm weather it has spent up to two months confined to cells chambered out in damp moss packed in a glass jar. The glass reveals single, double, and communal apartments with rounded walls in the moss, smoothed and compacted with mucus by the slugs. Some emerge to feed again, and to breed normally.

A. intermedius will diligently skeletonize saturated dead leaves, and is very easily kept in captivity for long periods without attention. It may not achieve pest status, and it tends to be dispersed while the other species are gregarious, but it is hardy, and it may be more successful on

lighter and less hospitable soils. In areas of rather poor country, as in many woodlands, and in large parts of the Scottish Highlands, it is likely to be the only species of the group to be found.

NOMENCLATURE

The original description and figures of *Arion hortensis* by Férussac (1819, 65; pl. 2, figs 4–6) suggest **R**, without excluding **A**. The blue-black banding pattern is described, and black tentacles with some transparency at the base, but there is no mention of any reddish tint. Either species therefore could provide some of the forms which have been regarded as typical *A. hortensis*. It would be reasonable conjecture to interpret Férussac's main description, with figs 4–5, as **R**, and his α , with fig. 6, as **A**, their distinctness being supported by his observation that the two varieties appear almost separately and successively in the same places.

Efforts to establish conclusively the identity of the true *A. hortensis* Férussac, and to name the other species, were being made with the help of the late Dr. C. O. van Regteren Altena, whose unfortunate death has delayed the production of a final solution to the problem. In 1976 Altena was able to examine material from the Paris Museum, including two original specimens of Férussac from 'montagnes des env. de Clermont'. They were shrunk and faded, 'but the lateral bands are dimly seen and the right band is arched over the respiratory orifice'. Opening the larger specimen, with permission, he found it to be a nearly mature **R**.

ACKNOWLEDGEMENTS

Sincere thanks are offered for the kindness and patience of friends who have supplied slugs, or have allowed slugs to be examined in their houses; also for the helpful interest shown and the essential encouragement given by the late Dr. C. O. van Regteren Altena in 1976, and by Mr. A. E. Ellis and Mr. J. F. Peake in earlier years.

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THE HABITATS OF MOLLUSCA IN THE CENTRAL HIGHLANDS OF SCOTLAND

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Abstract: From a chosen study area of almost 70 000 km² in the central Highlands of Scotland, 76 species of Mollusca were obtained. The detailed habitat distribution of these species is described in the various plant communities and freshwater environments. The most important factors determining distribution are calcium, water and habitat structure.

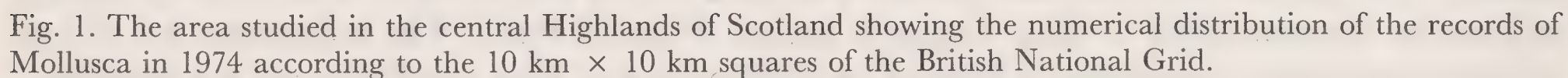
Britain comprises two lands divided by a line from Devon to Yorkshire. To the south and east are the fertile plains which belong with northern France. To the north and west is the infertile hill country, a remnant of the great Caledonian orogenic belt which extended to western Scandinavia. Habitat contrasts between the two regions are related not only to substrate differences but are greatly enhanced by climatic factors. High winds, heavy cloud cover and rain in the north-west keep summer temperatures low and the growing season short at elevated stations. The natural tree-line was probably around 650 m and climatic conditions on British mountains are analogous to those on arctic coasts (Pearsall 1950). The mountains are of low altitude and alpine conditions of limited precipitation and high insolation do not develop.

There is strong evidence that trees were formerly widespread in mountain Britain to at least 600 m and up to a maximum of 900 m in the central Highlands. The bleak grasslands, moorlands and bogs which we see today have largely been produced by the activities of man and of grazing animals. Forest clearance by man was well under way even in Neolithic times. Grazing by sheep and deer has prevented regeneration of the forests and is a constant drain on soil fertility because shallow rooting grasses do not assist in the release of minerals from the parent rock as trees would do. However, tree farming of softwoods for rapid return may be even more demanding than grazing practices.

It is fortunate that the Scottish Highlands have been the subject of much recent plant ecological work. The monograph of McVean and Ratcliffe (1962) gives a wealth of detailed information. In addition the critical treatment edited by Burnett (1964) has made information about Scottish vegetation more readily available than for any other part of Britain. An understanding of the habitat distribution of Mollusca in semi-natural vegetation in the Scottish Highlands can be developed against a clear ecological background. There is little previously published information of this sort. Boycott (1934) was most familiar with England and thought that 'things might appear rather differently to Scotch ... naturalists'.

DISTRIBUTION OF THE MOLLUSCA

The region studied is situated in the central Highlands of Scotland or Grampian Mountains (Fig. 1) lying in parts of the old counties of Perthshire, Argyllshire, Inverness-shire, Aberdeenshire and Angus. It takes in well known peaks such as Ben Lui, Ben Lawers, Ben



Combination of these results with existing information from the Conchological Society's Mapping Scheme (kindly provided by Dr. M. P. Kerney) gave the faunal list for the area (Table 1). The numerical distribution of the records by 10 km \times 10 km squares of the British National Grid (as obtained up to 1974) is shown on the map (Fig. 1). Detailed results have now been published (Kerney 1976). The Breadalbane to Clova is the richest area, due to the occurrence of limestone and calcareous schists and fertile lowlands. Particularly poor areas are Rannoch Moor and the higher parts of the Cairngorms where oligotrophic bogs and moorland are widespread.

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BISHOP: HIGHLAND MOLLUSCA

TABLE 1

Occurrence of species of molluscs obtained in the 69 10 km × 10 km squares sampled in the central Highlands of Scotland. Columns 1–4 give the occurrence of individual species arranged in four classes according to the total number of species per square and column 5 gives the total number of occurrences. Column 6 gives the maximum deviation from the expected cumulative frequency distribution in the Kolmogorov-Smirnov one-sample test (Siegel, 1956), italics $P < 0.05$, bold $P < 0.01$.

	Frequency class of square				Total	D_{\max}
	1–7	8–15	16–31	32–54		
Number of squares	23	21	14	11	69	
<i>Arion ater</i> (L.)	17	17	12	11	57	0.041
<i>Oxychilus alliarius</i> (Miller)	9	15	11	11	46	0.138
<i>Pisidium casertanum</i> (Poli)	11	14	11	10	46	0.094
<i>Arion intermedius</i> Normand	9	13	12	11	45	0.149
<i>Nesovitrea hammonis</i> (Ström)	6	15	13	10	44	0.197
<i>Deroceras reticulatum</i> (Müller)	5	13	10	11	39	0.205
<i>Columella aspera</i> Waldén	9	11	11	6	37	0.097
<i>Euconulus fulvus</i> (Müller)	5	7	13	11	36	0.304
<i>Arion subfuscus</i> (Draparnaud)	9	9	9	9	36	0.138
<i>Vitrea crystallina</i> (Müller)	4	6	13	11	34	0.347
<i>Aegopinella pura</i> (Alder)	3	5	13	11	32	0.388
<i>Punctum pygmaeum</i> (Draparnaud)	3	7	9	10	29	0.293
<i>Cochlicopa lubrica</i> (Müller)	–	8	10	10	28	0.352
<i>Vitrina pellucida</i> (Müller)	2	5	11	10	28	0.388
<i>Aegopinella nitidula</i> (Draparnaud)	–	7	10	10	27	0.378
<i>Arion circumscriptus</i> Johnston	–	8	8	9	25	0.333
<i>Lymnaea truncatula</i> (Müller)	2	5	8	10	25	0.358
<i>L. peregra</i> (Müller)	5	7	5	8	25	0.161
<i>Deroceras laeve</i> (Müller)	2	5	8	10	24	0.358
<i>Limax marginatus</i> Müller	5	5	6	8	24	0.221
<i>Pisidium personatum</i> Malm	3	4	7	8	22	0.320
<i>Discus rotundatus</i> (Müller)	–	2	8	11	21	0.542
<i>Arion hortensis</i> Férussac	1	3	6	9	19	0.427
<i>Ancylus fluviatilis</i> Müller	3	5	2	8	18	0.285
<i>Carychium minimum</i> Müller	2	–	7	9	18	0.527
<i>Arion silvaticus</i> Lohmander	4	1	7	5	17	0.343
<i>Carychium tridentatum</i> (Risso)	1	1	6	9	17	0.520
<i>Vertigo substriata</i> (Jeffreys)	2	4	5	6	17	0.285
<i>Arianta arbustorum</i> (L.)	–	3	5	8	16	0.450
<i>Columella edentula</i> (Draparnaud)	–	–	5	10	15	0.638
<i>Vitrea contracta</i> (Westerlund)	–	2	3	10	15	0.507
<i>Acanthinula aculeata</i> (Müller)	–	–	5	9	14	0.638
<i>Oxychilus cellarius</i> (Müller)	–	1	4	9	14	0.566
<i>Arion fasciatus</i> (Nilsson)	–	2	7	4	13	0.484
<i>Cepaea hortensis</i> (Müller)	–	–	5	7	12	0.638
<i>Pisidium milium</i> Held	–	2	1	9	12	0.591
<i>Trichia hispida</i> (L.)	–	–	3	9	12	0.638
<i>Cepaea nemoralis</i> (L.)	–	–	2	9	11	0.659
<i>Clausilia bidentata</i> (Ström)	–	1	2	8	11	0.568
<i>Pisidium subtruncatum</i> Malm	–	3	1	7	11	0.477
<i>Limax cinereoniger</i> Wolf	5	2	1	2	10	0.167
<i>Pisidium nitidum</i> Jenyns	–	1	3	6	10	0.538
<i>P. hibernicum</i> Westerlund	–	1	3	5	9	0.527
<i>Spermodea lamellata</i> (Jeffreys)	–	1	2	6	9	0.527
<i>Cochlicopa lubricella</i> (Porro)	–	1	2	5	8	0.513
<i>Deroceras agreste</i> (L.)	–	1	5	2	8	0.513
<i>Lauria cylindracea</i> (da Costa)	–	–	1	7	8	0.716
<i>Trichia striolata</i> (C. Pfeiffer)	–	–	1	7	8	0.716

	Frequency class of square				Total	D _{max}
	1-7	8-15	16-31	32-54		
<i>Zenobiella subrufescens</i> (Miller)	—	—	2	6	8	0.638
<i>Pisidium lilljeborgi</i> Clessin	—	2	2	3	7	0.352
<i>Limax maximus</i> L.	—	—	—	6	6	0.841
<i>L. tenellus</i> Müller	—	1	1	4	6	0.507
<i>Oxyloma pfeifferi</i> (Rossmässler)	—	—	1	5	6	0.674
<i>Zonitoides excavatus</i> (Alder)	—	2	2	2	6	0.333
<i>Z. nitidus</i> (Müller)	—	—	1	3	4	
<i>Bathyomphalus contortus</i> (L.)	—	—	1	2	3	
<i>Ena obscura</i> (Müller)	—	—	—	3	3	
<i>Pisidium obtusale</i> (Lamarck)	—	1	1	1	3	
<i>Sphaerium corneum</i> (L.)	—	—	1	2	3	
<i>Balea perversa</i> (L.)	—	—	—	2	2	
<i>Planorbis carinatus</i> Müller	—	—	—	2	2	
<i>Pyramidula rupestris</i> (Draparnaud)	—	—	—	2	2	
<i>Vertigo antivertigo</i> (Draparnaud)	—	—	—	2	2	
<i>Gyraulus albus</i> (Müller)	—	—	1	—	1	
<i>Leiostryla anglica</i> (Wood)	—	—	—	1	1	
<i>Lymnaea palustris</i> (Müller)	—	—	—	1	1	
<i>Margaritifera margaritifera</i> (L.)	—	—	—	1	1	
<i>Milax budapestensis</i> (Hazay)	—	—	—	1	1	
<i>Monacha granulata</i> (Alder)	—	—	—	1	1	
<i>Pisidium pulchellum</i> Jenyns	—	—	—	1	1	
<i>Potamopyrgus jenkinsi</i> (Smith)	—	—	—	1	1	
<i>Sphaerium lacustre</i> (Müller)	—	—	—	1	1	
<i>Vallonia excentrica</i> Sterki	—	—	—	1	1	
<i>Valvata piscinalis</i> (Müller)	—	—	—	1	1	
<i>Vertigo lilljeborgi</i> Westerlund	—	—	—	1	1	
<i>V. pusilla</i> Müller	—	—	—	1	1	
Number of species	25	44	58	5	76	

lilljeborgi, *Limax tenellus* and *Zonitoides excavatus* are relatively uncommon in calcareous lowland eastern Britain but are particularly at home in the Highlands. Species whose frequency distribution deviated significantly from expectation were those with a clear increase in population density in base rich habitats.

THE FOREST ZONE

Little remains of the original forest cover of the central Highlands which extended to 600–800 m. Reconstruction of the original woodland distribution (McVean and Ratcliffe 1962) suggests that the major part of the region was pine forest with birch, whilst in the west-central Highlands oak forest with birch predominated. Today the majority of the vegetation consists of grasslands, dwarf-shrub heaths, mires and bogs. The distribution of oak and pine within a limited area is related to edaphic factors, oak growing on the richer alluvial and colluvial soils with pines on coarser stony soils with peat formation.

Pine woodland. Steven and Carlisle (1959) have presented an excellent account of the native pine (*Pinus sylvestris* L.) woods of Scotland. The fine woods of Deeside and Speyside lie largely outside the area surveyed, though Glen Feshie (British National Grid Reference 27/8493) was examined. To the west, excursions were made to the Black Wood of Rannoch (27/5856), the Old Wood of Meggernie (27/5545), Black Mount (27/2841) and Tyndrum (27/3328). Pure stands of pine were virtually free of Mollusca. Specimens of *Limax cinereoniger* could sometimes

be obtained by rolling large logs. Where amelioration of the habitat occurred through interspersing of birch or flushing further species could be found.

Birch and oak woodland. Three taxa of birch are recognized in Scottish forests and their separation is difficult. Present birch woods often mark the site of degenerated pine or oak woods, whilst regenerating birch scrub may colonize open moor or grassland. The native Highland oak is *Quercus petraea* (Mattuschka) Liebl. and it often forms mixed stands with birch. Two associations can be recognized according to the composition of the field layer, although there is complete intergradation.

The *Vaccinium*-rich birch wood association often has *Vaccinium myrtillus* L. (bilberry), *Luzula sylvatica* (Huds.) Gaud. (woodrush) or *Pteridium aquilinum* (L.) Kuhn (bracken) dominating the woodland floor. *Vaccinium vitis-idaea* L. (cowberry), *Lonicera periclymenum* L. (honeysuckle) and *Melampyrum pratense* L. (cow-wheat) often occur. The soil pH is approximately in the range 4.5–5.5. Fragments of this kind of woodland are widespread in the Highlands. Some examples examined were Inverloch (27/2028), Glen Falloch (27/3320), Falls of Tummel (27/9060) and Talla Bheith (27/5657). The molluscs of these woodlands are *Aegopinella nitidula*, *A. pura*, *Arion ater*, *A. intermedius*, *A. silvaticus*, *A. subfuscus*, *Columella aspera*, *Discus rotundatus*, *Euconulus fulvus*, *Limax cinereoniger*, *L. marginatus*, *Nesovitrea hammonis*, *Oxychilus alliarius*, *Vitrea crystallina*, *Vitrina pellucida* and *Zonitoides excavatus*.

The herb-rich birch and oakwood association is often grassy. *Vaccinium* is absent and herbs such as *Endymion non-scriptus* (L.) Garcke (bluebell), *Anemone nemorosa* L. (wood anemone), *Conopodium majus* (Gouan) Lor. (pignut), *Primula vulgaris* Huds. (primrose) and *Viola riviniana* Rchb. (violet) are often prominent. *Corylus avellana* L. (hazel) is common. The soil pH is approximately in the range 5.0–6.5. Fragments of this type of vegetation are common in the Highlands and often occur along stream sides where some mineral enrichment is present. Some examples examined were Linn of Muick (37/3389), Crom Allt (27/3331), Bridge of Cally (37/1452), Allt Coire Chaorach (27/4527), Creag Liath (27/7686), Glen Feshie (27/8689) and Inchgarth (27/7651). Better developed woodland with a good litter could also be examined, as at Carbane Castle (27/6748), Claggan (27/7138), Invervar (27/6547) and Falls of Lochay (27/5335).

The fauna of the herb-rich birch and oakwood association included all the species of the *Vaccinium*-rich birchwood association with the addition of *Carychium minimum*, *C. tridentatum*, *Acanthinula aculeata*, *Arianta arbustorum*, *Arion circumscriptus*, *A. fasciatus*, *A. hortensis*, *Cepaea hortensis*, *C. nemoralis*, *Clausilia bidentata*, *Cochlicopa lubrica*, *C. lubricella*, *Columella edentula*, *Deroceras reticulatum*, *Ena obscura*, *Lauria cylindracea*, *Leiostyla anglica*, *Limax tenellus*, *Oxychilus cellarius*, *Punctum pygmaeum*, *Spermodea lamellata*, *Trichia hispida*, *Vertigo pusilla*, *V. substriata*, *Vitrea contracta* and *Zenobiella subrufescens*.

Mixed deciduous woodland. In the Tay valley on fertile brown loams are to be found oak-ash-elm woods, sometimes with naturally regenerating sycamore. There is often a field layer of *Mercurialis perennis* L. (dog's mercury) or *Allium ursinum* L. (ramsons). The soil pH is in the range 6.5–7.5. Examples examined were Bolfracks (27/8047) and Killiecrankie (27/9162). The woods have a very rich fauna with possibly all the species previously mentioned with the exception of *Columella aspera* and *Zonitoides excavatus* and the addition of *Limax maximus* and *Trichia striolata*.

Fern-rich willow scrub. Patches of scrub may be present particularly in boulder beds or scree slopes. Though often ravaged by grazing animals, they may carry a fauna like that of the *Vaccinium*-rich birch wood association. Examples were examined at Drumchorrie (27/9359), Braes of Foss (27/7455) and Glen Doll (37/2875). The Cairngorm juniper scrub was not examined.

Rock ledges. Shady well watered rock ledges of calcareous schist which are inaccessible to grazing animals act as refuges for the herbs and snails of the herb-rich birch and oakwood association amid an otherwise barren landscape. Such situations are unfortunately scarce but yield an interesting fauna (Table 2), *Arianta arbustorum* being prominent.

TABLE 2.

The mollusc fauna of rock ledges in the central Highlands. 1: Falls of Tarf, 460 m (27/982797); 2: Ciochan Beinn Laoigh, 610 m (27/261276); 3: Creag an Lochain, 690 m (27/591408), compare Smith in Dance, (1972).

	1	2	3
<i>Aegopinella nitidula</i>	+	-	-
<i>A. pura</i>	+	-	-
<i>Arianta arbustorum</i>	+	+	+
<i>Arion ater</i>	-	+	-
<i>Carychium minimum</i>	-	+	-
<i>C. tridentatum</i>	-	+	-
<i>Clausilia bidentata</i>	-	+	+
<i>Columella aspera</i>	+	+	-
<i>C. edentula</i>	-	+	+
<i>Deroceras laeve</i>	-	+	-
<i>Discus rotundatus</i>	-	-	+
<i>Euconulus fulvus</i>	-	-	+
<i>Limax marginatus</i>	-	+	-
<i>Nesovitrea hammonis</i>	+	+	+
<i>Oxychilus alliarius</i>	+	+	+
<i>Punctum pygmaeum</i>	-	+	-
<i>Trichia hispida</i>	-	-	+
<i>Vitrea crystallina</i>	+	+	+
<i>Vitrina pellucida</i>	+	+	+

Grasslands and dwarf-shrub heaths. In terms of area covered and economic importance these communities dominate the Highland scene. To the malacologist however, mile after mile of oligotrophic grassland and heath presents a dismal picture. *Arion ater* appears to be the only species which can flourish under these conditions. Other slugs may become important in the richer grasslands, especially when shelter in the form of stones or tussocks of vegetation is present. Of particular interest is the occurrence of *Deroceras agreste*, first recognized in mainland Scotland from the Moray Firth region (Kellock 1970) and now found to be widespread though local in the central Highlands. Other slugs of the mesotrophic grasslands are *Deroceras reticulatum*, *Arion circumscriptus*, *A. fasciatus*, *A. silvaticus*, *A. hortensis*, *A. intermedius* and *A. subfuscus*. Snails are hard to find in the grasslands and heaths, and more success is had when a low clump of birches or willows provides a little leaf litter or a patch of rushes (*Juncus effusus* L.) traps moist decaying vegetation. Such places are here considered with woodlands and mires respectively. Prolonged searching in grasslands and heaths in localities too numerous to list yielded the following snails: *Euconulus fulvus*, *Punctum pygmaeum*, *Nesovitrea hammonis*, *Columella aspera*, *Aegopinella nitidula*, *Cochlicopa lubrica*, *C. lubricella* and *Carychium tridentatum*.

Walls. In the central Highlands the presence of *Balea perversa*, *Pyramidula repestris* and *Vallonia excentrica* seemed to depend on these man-made structures.

THE WETLANDS

Swamp vegetation develops in hollows adjacent to open water, exists on permanently or seasonally submerged soil and is dominated by emergent aquatic plants. Marshes (on mineral soil) and fens (on peat soil) are only seasonally or periodically submerged and are dominated by marsh plants. They vary according to water chemistry and substrate composition. Flushes (on mineral soil) and mires (soligenous bogs) are analogous to marshes and fens but depend on the lateral seepage of water under gravity and receive a terrestrial mineral enriched water supply. Bogs (ombrogenous bogs) depend on rain for their water supply and consequently have a very low nutrient status. Although wetland vegetation is often locally distinct, intermediates exist emphasizing that variation is continuous.

Swamps, marshes and fens. These habitats develop rarely in the area as loch shores are often stony and rivers fast flowing. The fens and marshes which do develop are usually mesotrophic (soil pH 4.5–6.0) or 'poor-fens'. Firbrush Point (27/6033) and Loch Dochart (27/4025) were examined. The molluscs of these habitats include *Carychium minimum*, *Lymnaea truncatula*, *Arion ater*, *A. intermedius*, *Cochlicopa lubrica*, *Columella edentula*, *Deroceras laeve*, *Euconulus fulvus*, *Nesovitrea hammonis*, *Oxychilus alliarius*, *Oxyloma pfeifferi*, *Punctum pygmaeum*, *Vertigo antivertigo*, *V. lilljeborgi*, *V. substriata*, *Vitrea crystallina*, *Pisidium casertanum*, *P. obtusale* and *P. personatum*. Kevan and Waterstone (1933) give further details of the Mollusca of Highland fens.

Mires and bogs. The vegetation of mires and bogs in the Highlands has been reviewed by Ratcliffe (in Burnett 1964). As far as molluscs are concerned, soil fertility is the over-riding factor. Oligotrophic bogs support only *Arion ater* and *Pisidium casertanum*. Mires vary from poor to rich in molluscs according to base status without appreciable changes in the appearance of the vegetation, although basiphilous herbs and bryophytes are indicative. Two common vegetation types were studied, *Juncus effusus* – *Sphagnum* mire and *Molinia* – *Myrica* mire.

Examples of *Juncus effusus* – *Sphagnum* mires were examined at Killin (27/5645) and Glen Dochart (27/4533). The fauna was very similar to that of the fen sites but lacked *Columella edentula*, *Vertigo lilljeborgi* and *Zonitoides nitidus* and contained in addition *Aegopinella pura*, *Cepaea hortensis*, *Columella aspera*, *Deroceras agreste*, *D. reticulatum* and *Zonitoides excavatus*.

Examples of *Molinia* – *Myrica* mires studied were at Keltneyburn (27/7751), Glen Errochty (27/7764), Mullinavadie (27/7161) and Tummel Bridge (27/7359). The fauna was very similar to that of *Juncus effusus* – *Sphagnum* mire with the addition of *Aegopinella nitidula* and *Vitrea contracta* and a general lack of *Pisidium* species.

THE MONTANE ZONE

The montane zone is here considered to lie above 750 m (2450 ft) where habitats suitable for molluscs are few. The vertical range of molluscs in the Highlands has been ably discussed by Dance (1972b). There are no new species in the montane zone but an impoverished lowland fauna is present including *Aegopinella pura*, *Arianta arbustorum*, *Arion ater*, *A. intermedius*, *A. subfuscus*, *Clausilia bidentata*, *Columella edentula* agg., *Euconulus fulvus*, *Limax marginatus*, *Nesovitrea hammonis*, *Vitrina pellucida* and *Pisidium casertanum*. The boreo-alpine species *Columella columella* (Benz), *Discus rudersatus* (Férussac) and *Nesovitrea petronella* (Pfeiffer) have a fossil record in Britain but it seems unlikely that they have survived. If they have, it will be on an ungrazed rock ledge or in a calcareous flush high above a remote Highland glen.

FRESHWATER HABITATS

The waters of the region are all more or less deficient in calcium. The distribution of the freshwater molluscs is largely controlled by substrate and water flow. The freshwater species

which overlap into wetland habitats are those of wide tolerance found even in small peaty water bodies and are *Lymnaea peregra*, *L. truncatula*, *Pisidium casertanum*, *P. obtusale* and *P. personatum*. Rocky torrents which are scoured by gravel and exposed lake shores subject to extreme wave action contain no molluscs. When these conditions ameliorate sufficiently, *Ancylus fluviatilis* and *Lymnaea peregra* may be found. The pearl mussel, *Margaritifera margaritifera*, was once common in the River Tay and its tributaries (Coates 1922) but has apparently become scarce in recent years. The introduced *Potamopyrgus jenkinsi* has so far made little encroachment, being reported only from the Tay below Aberfeldy (27/9953). In the less acidic weedy pools, such as at Drumore (37/1660) and Blair Castle (27/8666), are to be found *Valvata piscinalis*, *Bathyomphalus contortus*, *Gyraulus albus*, *Planorbis carinatus*, *Sphaerium corneum* and *S. lacustre*. *Lymnaea palustris* is remarkably scarce.

The *Pisidium* fauna is of considerable interest, ten species being represented. The habitat preferences will not be elaborated here, the situation being entirely comparable to that described by Oldham (1932) for northern Scotland. Meier-Brook (1963) obtained an identical fauna in the Black Forest and the Vosges. *P. conventus* (Clessin) was not found by the author and it might be obtained more commonly if deep dredging of the larger lochs were carried out.

DISCUSSION

It is of interest to compare the faunal list for the central Highlands reported here with that for the Southern Uplands (Kerney 1974). The central Highlands has a poorer though very similar fauna, the ten most frequent species on each list however including only three in common. The species of the most base poor habitats are more frequent because there is often little else to find in the Highlands. *Columella aspera*, *Euconulus fulvus*, and *Nesovitrea hammonis* are a constant feature of the ubiquitous oligotrophic to mesotrophic mires and woodlands, as they are in similar habitats in Ireland (Bishop 1976) and Sweden (Waldén 1969; Wäreborn 1969).

Inspection of the faunal lists from different vegetation types shows that there are very few species which are restricted to particular plant habitats. *Vertigo lilljeborgi* occurs only in mesotrophic fens subject to flooding (compare Dance 1972a) and is the most particular in its requirements. All the other species may occur in more than one vegetation type, although the associations may be characteristic. There would be little to surprise Boycott (1934) in this account of the occurrence of molluscs in Highland habitats. The most important environmental gradients are undoubtedly calcium, water and habitat structure (shelter). *Columella aspera* can be added as a second calcifuge species along with *Zonitoides excavatus*.

The lower limit of the tolerated range with regard to calcium is hard to define as threshold population densities are very small. Acidity and calcium may be rather indefinitely related (Wäreborn 1969) although Ratcliffe (in Burnett 1964) found it convenient to use the two interchangeably in his definition of oligotrophic, mesotrophic and eutrophic levels of fertility. Critical levels for molluscs are around 1 part per million (ppm) dissolved calcium in freshwater, 100 ppm exchangeable calcium in soil, 1000 ppm in litter and pH 3.5–4.0. This means that limited populations occur in the more fertile oligotrophic habitats, the upper limit of which is defined by Ratcliffe as being 4 ppm in water, 300 ppm in soil and pH 5.0.

Although the role of calcium is crucial, its mode of action is complex and difficult to elucidate. The facts of the matter must be considered for each species in turn and no sweeping generalizations can be made. Frömming (quoted by Macan 1950) concluded that the poor fauna of acid peaty water is due to poor food supply rather than any chemical factor. Clearly many species of molluscs are not limited in this way and require a high intake of calcium as a physiological necessity. Molluscs which eat vascular plants may be limited by the absence of suitable food species in oligotrophic habitats but the majority of snails obtain nourishment from the micro-organisms of decay. Calcium will buffer deleterious organic acids and hence

encourage bacterial action producing more food. The calcium content of the food supply is likely to be as important to snails as the calcium component of the physical environment. Some ingenious work will be necessary to sort out the response to different calcium to protein ratios in the natural diet of individual mollusc species.

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ANATOMICAL NOTES ON SOME JAVANESE *AMPHIDROMUS* (PULMONATA: CAMAENIDAE)

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Abstract: The anatomy of *Amphidromus palaceus* (Mousson), *A. javanicus* (Sowerby), *A. heerianus* (Pfeiffer) and *A. porcellanus* (Mousson) is described. The internal ornament of the penial complex can be used to characterize each of these four species.

The family Camaenidae is a group of helicacean land snails without dart sacs or accessory vaginal glands on the genitalia. It has members in tropical or sub-tropical America, Asia and Australia. Its relationship to the other helicacean families is unclear. The American camaenids are well known anatomically (Wurtz, 1955) and an analysis of their phylogenetic relationships, present distribution and fossil record suggests a Cretaceous origin for the family.

Anatomical information about Asian and Australian camaenids is fragmentary and widely scattered through a literature which is often inadequate for a proper understanding of the systematics of the group. Every effort should be made to improve our knowledge of this family which promises to be crucial for an appreciation of helicacean evolution and oriental biotic history.

The present contribution relates to the genus *Amphidromus* Albers. Laidlaw and Solem (1961) have presented a masterly appraisal of the group in the light of the available evidence and have recognized 74 species. Most of these are known from shells alone, only about 8 recognizable taxa having been dissected. Through the kindness of M. Djajasasmitta of Museum Zoologicum Bogoriense I have been able to re-examine *A. palaceus* (Mousson) and *A. porcellanus* (Mousson) and to describe the anatomy of *A. javanicus* (Sowerby) and *A. heerianus* (Pfeiffer) for the first time.

DESCRIPTIONS

1. *Amphidromus palaceus* (Mousson) This species was studied by Collinge (1901) but some additional points are made here.

Pallial complex. This is of sigmurethran pattern with the apical angle of the lung and ureter not extending beyond the kidney. The ureter is closed for the full length of the lung. The lung is about 1.5 times the length of the kidney. The kidney is about 15 times as long as broad at half length and four times the length of the pericardium. This description is common to all the four species dissected.

Retractor muscles. The left ocular retractor passes through the penioviducal angle. The left and right compound retractors and the tail fan arise separately at the columellar insertion, while the buccal retractor arises from the right compound retractor (Fig. 1A). Collinge (1901) is not specific on this point, an analogous condition being observed in all four species.

Digestive system. The jaw is thin and weak with low flat ribs (Fig. 1B). The radula has

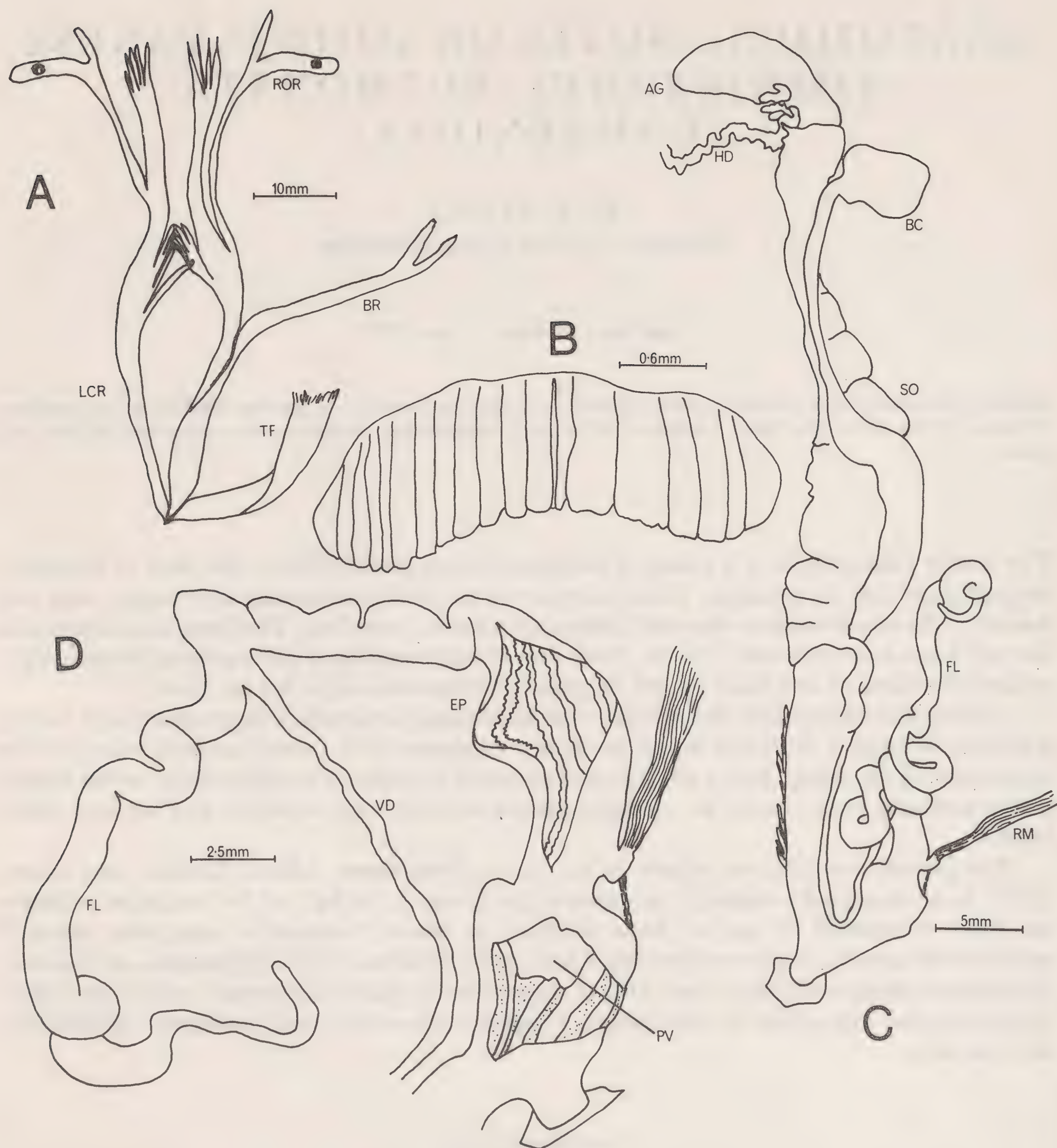


Fig. 1. *Amphidromus palaceus* (Mousson) Cibodas, W. Java from a mountain garden at 1400 m S. Adisoemarta leg. A free retractor muscles, B jaw, C reproductive system, D penial complex. AG albumen gland, BC bursa copulatrix, BR buccal retractor displaced to right, EP epiphallus, FL flagellum, HD hermaphrodite duct, LCR left compound retractor muscle, PV penial verge, RM penial retractor muscle, ROR right ocular retractor muscle, SO spermoviduct, TF tail fan, VD vas deferens.

markedly V-shaped rows of about 170 teeth. The teeth (Fig. 2A) are gouge shaped with short broad base plates and tend to the tricuspid condition. A similar pattern was present in all four species.

Reproductive system. The ovotestis occupies half a whorl and has numerous digitiform alveoli. The receptaculum seminalis is small and not extended as a talon. The upper male and female gonoducts are joined as a spermoviduct, the oviductal wall having weak transverse sacculations. The free oviduct is bound to the adjacent body wall with fibres. The stem of the bursa copulatrix

arises from the free oviduct and is very long (Fig. 1C). The sheath enclosing the penial complex is thin. A long epiphallic flagellum is present. The short penial retractor muscle is set at an oblique angle on a small epiphallic retractor caecum and is attached to the floor of the pulmonary cavity. A penial verge is present at the end of the short penis (Fig. 1D).

2. *Amphidromus javanicus* (Sowerby).

Digestive system. The radula tooth row has about 240 teeth, representatives being shown in Fig. 1B and the jaw in Fig. 3A.

Reproductive system. The penial retractor muscle is set obliquely but there is no retractor caecum (Fig. 3B). The penial verge is relatively small (Fig. 3C).

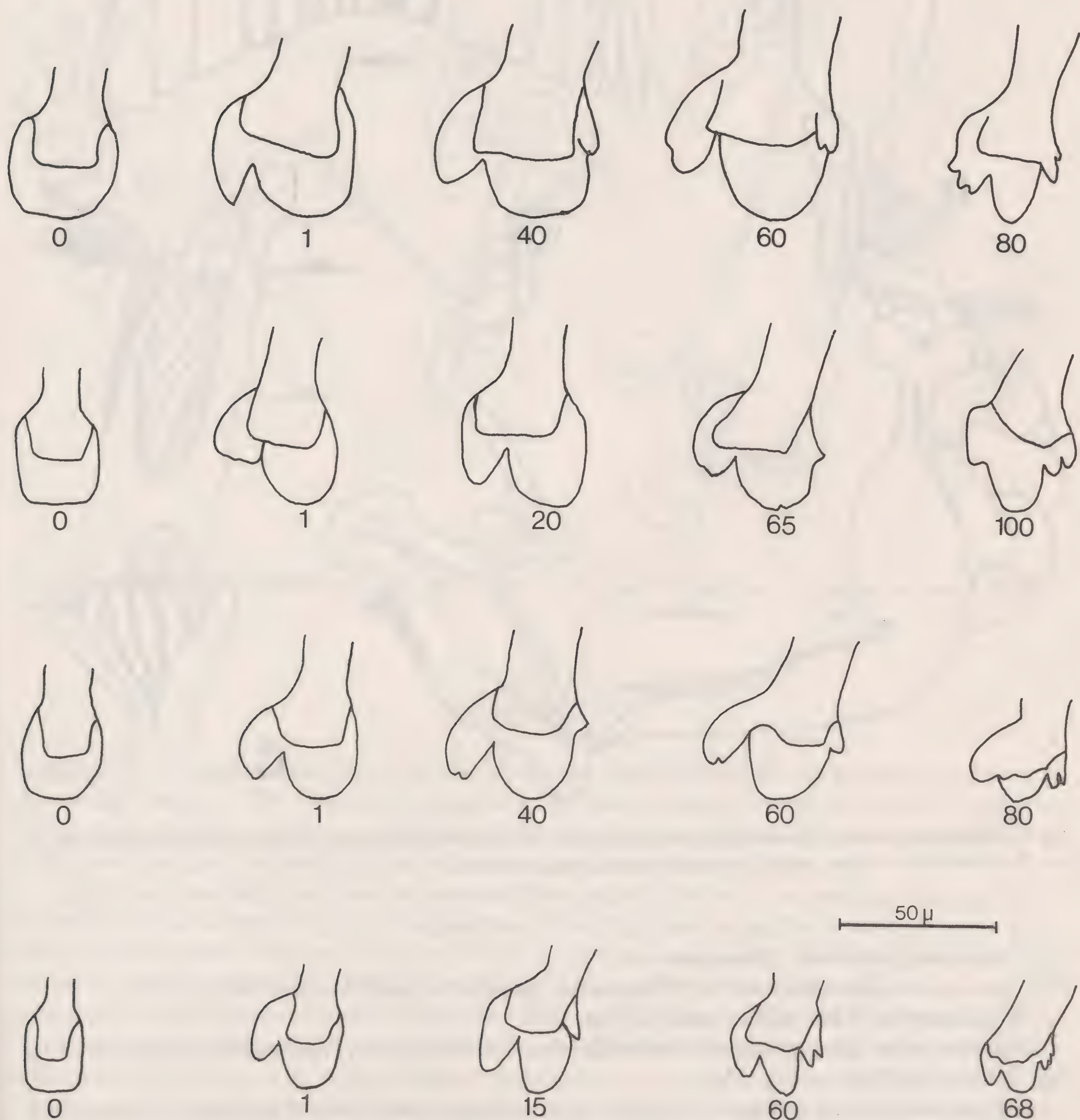


Fig. 2. Representative radula teeth of A *Amphidromus palaceus*, B *A. javanica*, C *A. heerianus*, and D *A. porcellanus*.

3. *Amphidromus heerianus* (Pfeiffer).

Pallial complex. This is illustrated in Fig. 5A.

Digestive system. The radula tooth row has about 170 teeth and representatives are shown in Fig. 2C and the jaw in Fig. 5B.

Reproductive system. The retractor caecum and penial verge are large (Fig. 4A, B). There is a broad low pillaster in the flagellum.

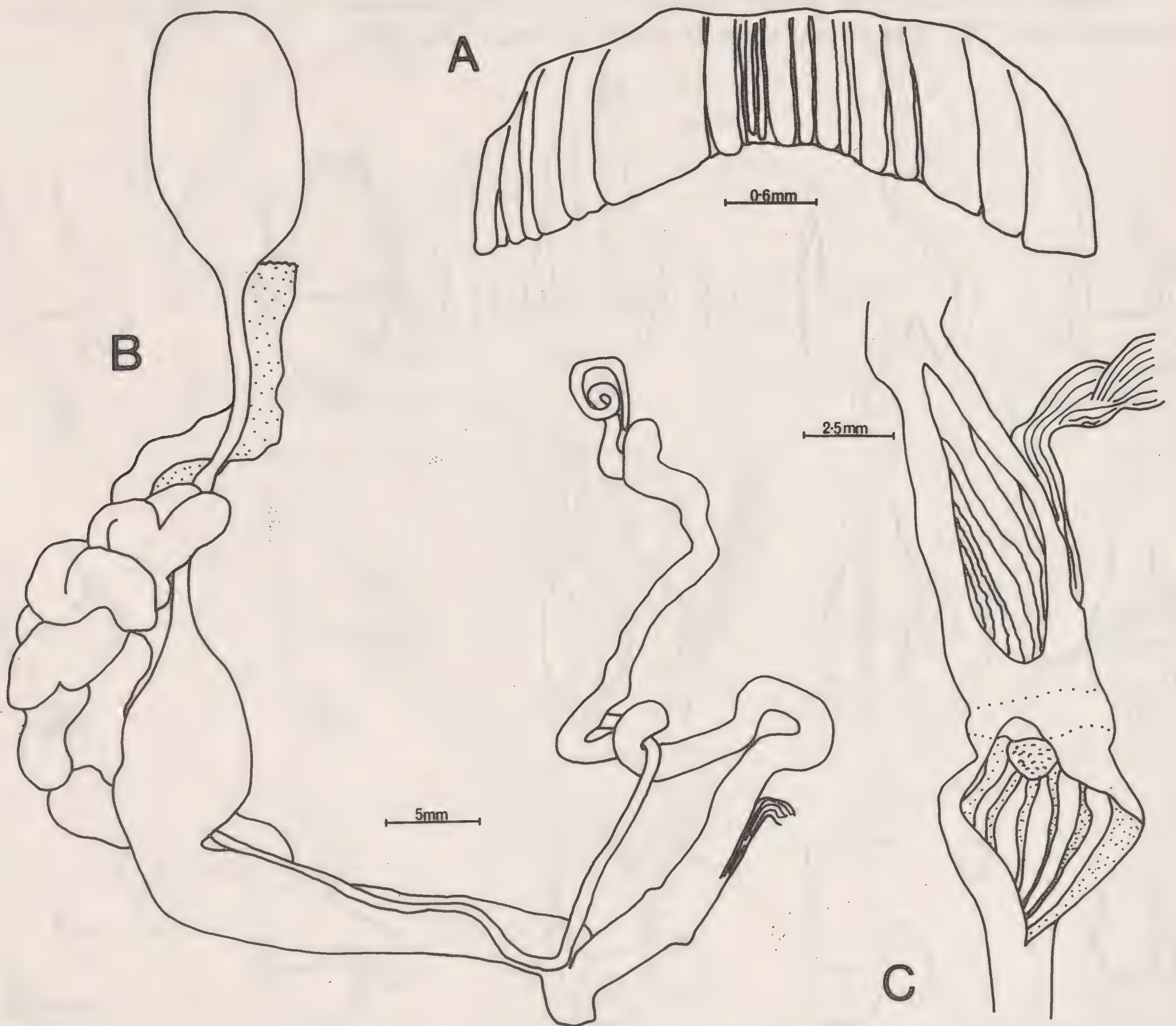


Fig. 3. *Amphidromus javanica* (Sowerby) Sukawayana Nature Reserve, Pelabuhanrata, W. Java. M. Djajasmita leg. A jaw, B reproductive system, and C proximal part of penial complex.

4. *Amphidromus porcellanus* (Mousson)

This species was first dissected by Wiegmann (quoted by Laidlaw and Solem, 1961).

Pallial complex. This is illustrated in Fig. 5C.

Digestive system. The radula tooth row has about 140 teeth and representatives are shown in Fig. 2D and the jaw in Fig. 5D.

Reproductive system. The flagellum is shorter than the proximal part of the penis in this species alone of the four studied (Fig. 5E). The penial verge is also different being in the form of a half clenched hand. The inside wall of the proximal part of the penis is smooth.



Fig. 4. *Amphidromus heerianus* (Pfeiffer) Citarik, Pelabuhanrata, W. Java. W. Harry leg. A reproductive system, B penial complex.

DISCUSSION

Each species of *Amphidromus* described here is readily characterized by the internal ornament of the penial complex. The characters thus provided are at least as useful as the shell in species recognition. Radulae might possibly be used for specific identification but are more difficult to study and interpret without the aid of a scanning electron microscope.

From the knowledge we have at present there appears to be no anatomical feature which uniquely characterizes the genus *Amphidromus*. The long narrow kidney and long bursa stem agree with the basic camaenid pattern. The buccal retractor arising from the left compound retractor (right in sinistral animals) probably represents a derived state but there is little comparative information on this character. The modification of the jaw and radula to the 'arboreal pattern' (Pilsbry, 1894) found also in the *Papuina* complex is undoubtedly a parallel adaptation to habitat. The penial complex is reminiscent of that of *Camaena* (Pilsbry, 1894, Pl. 18, Figs 1-4) and *Amphidromus* may represent an arboreal modification from a common antecedent. The present distribution of the two genera does not contradict this suggestion but further anatomical work is needed to confirm or refute it.

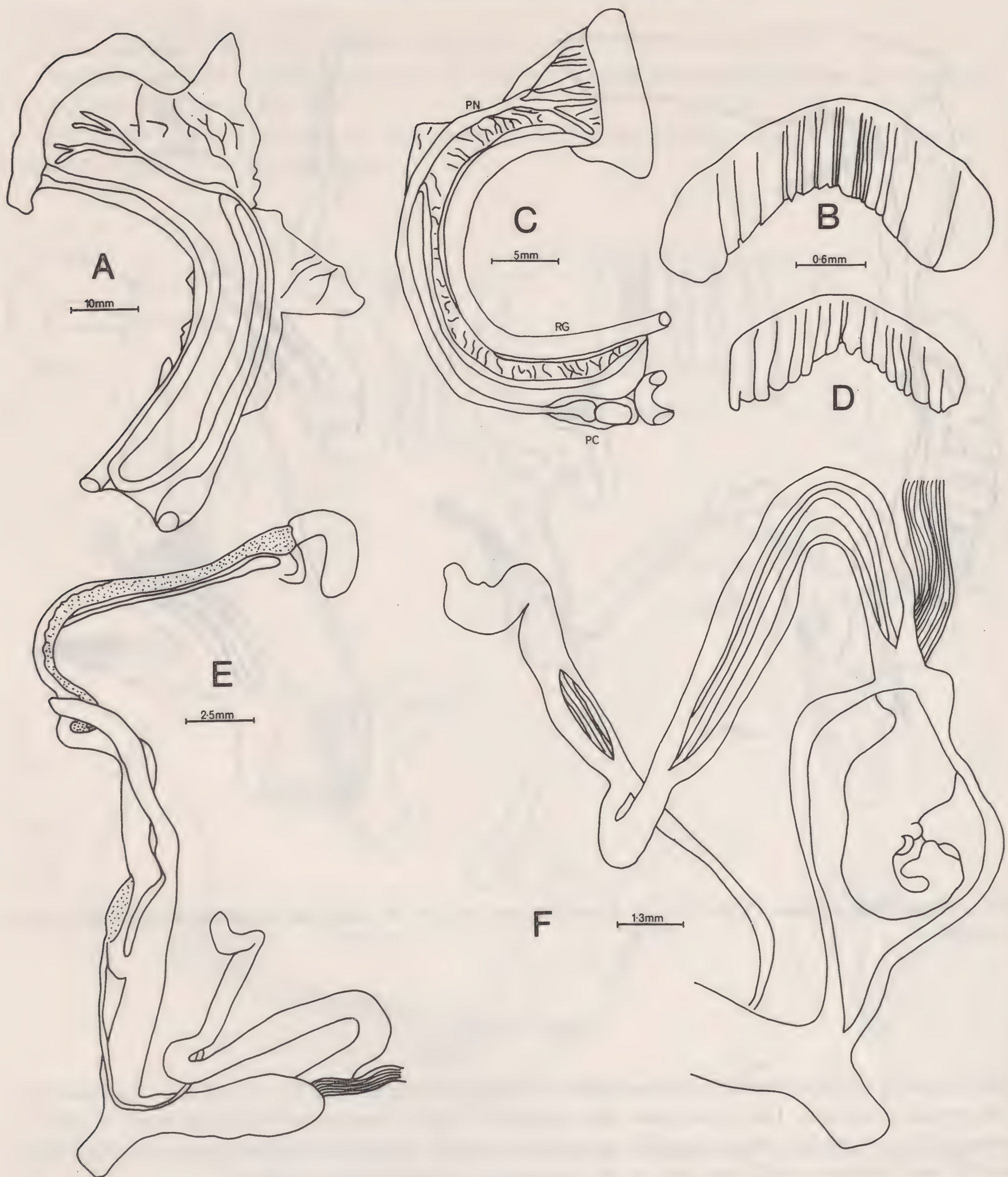


Fig. 5. *A. heerianus* A pallial complex, B jaw and *Amphidromus porcellanus* (Mousson) Botanic Garden, Bogor, W. Java. M. Djajasasmita leg. C pallial complex, D jaw, E reproductive system and F penial complex. PC pericardium, PN pulmonary vein, RG rear gut.

Syndromus Pilsbry was proposed for species of *Amphidromus* with the shell always sinistral, usually thin and unmarked with varix-stripes. *A. porcellanus* is placed in this taxon which Zilch (1959-60) treats as a subgenus.

Anatomically *A. porcellanus* differs from the other species dissected solely in details of the penial complex. The epiphallic flagellum is as short as the penis and the verge is long and recurved. These appear to be derived character states and the reduction in weight of the shell is

a further modification for the arboreal mode of life. It remains to be seen if these anatomical features are present in other *Syndromus* or if the shell type has arisen independently in different areas.

Beddomea Nevill is a generically distinct derivative of *Amphidromus* which occurs in southern India and Ceylon. Pilsbry (1901) showed that it differs from *Amphidromus* in having no endocone developed on the inner lateral teeth and in having the right ocular retractor passing to the right of both branches of the genitalia. Pilsbry stated that the buccal retractor arises from the right compound retractor but it is here shown that the buccal retractor arises from the left compound retractor in right handed animals of *Amphidromus*.

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SHAPE OF SHELL IN RELATION TO WEIGHT OF *MARGARITIFERA MARGARITIFERA* (L.) (BIVALVIA: MARGARITIFERIDAE)

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(Read before the Society, 16 April 1977)

Abstract: A method is described for calculating the volumes of closed valves of *Margaritifera margaritifera*. Dorsal arching of the shell is measured by Arching Index, a ratio expressing the proportionate rise of the dorsal margin above a line drawn from the umbo to the shell margin at the posterior termination of the ligament. Correlation between Weight/Volume (Specific Gravity) of the living bivalves and Arching Index is good. The heavier varieties of the species, length for length, have shells with strongly arched dorsal margins, with a trend towards straight or reflected ventral margins; they characterize waters subject periodically to a higher degree of turbulence than lighter varieties of this species, which have relatively straight 'hinge lines', stronger ligaments and shells with curved ventral margins. Washing away of young bivalves through turbulence during times of flood can locally limit the distribution of *M. margaritifera*. In stations near the margin of this physical limit individuals with higher Specific Gravities predominate, probably through selection, whereas in stations of lower water velocities the mode trends towards more active bivalves with a predominance of oval shells. The retention of a wide range of variation in shape of shell of the species constitutes a means by which its survival is ensured within the widely variable environments of fresh water, where there is continual re-distribution of populations by fish hosts. Evidence from the fossil record suggests that essentially the same pattern of variation provided similar 'insurance' in shells of Cenozoic and Mesozoic Unionidae, and in *Carbonicola*, of the non-marine Family Anthracosiidae of Carboniferous (late Palaeozoic) time.

INTRODUCTION : SHAPE OF SHELL AND ECOLOGICAL STATION

Considerable intra-specific variation in shape of shell is characteristic of members of the Unionacea in which the larva is parasitic on fishes (Haas 1940; 1969, p. N413). Variation is particularly wide in the pearl mussel *Margaritifera margaritifera* (Fig. 1). In this species each generation loses and regains contact with its environment which, dependent on fish movement and the time of release of the spat, may differ considerably from the previous one, both in the character of the bottom and especially in the degree to which the station is affected by maximum water velocities and concomitant danger of washing away through turbulence. The maintenance of a rather wide range of variation would therefore appear to be of survival value, if it can be shown that recurrent varieties have particular functional significance within the wide range of the environment of *M. margaritifera*.

It has been noted that, on the one hand, shells of many Recent unionid species, and on the other hand certain early faunas of the genus *Carbonicola* (Family Anthracosiidae) which characterized a variety of non-marine environments in Silesian (Upper Carboniferous) time, show two contrasted patterns of growth, which may both occur within single populations (Eagar 1948, p. 146)). In both the Recent and fossil shell groups each trend, or growth pattern, is correlated with the same environmental trend, in so far as the latter can be reconstructed from detailed studies of shell and sediment (Eagar 1961). In the first pattern of growth, the dorsum of the shell becomes arched and the ventral margin straightens and may become reflected (Fig. 1 A-D, F, G, I, L). This is associated with increase in the actual or potential maximum water velocity of the habitat (Eagar 1947, 1948, 1961). In the second trend, dorsal margins of shells approach straightness, or become straight, with the development of a relatively long 'hinge

line', whereas the ventral margins tend to show increasing degrees of curvature (Fig. 1 E, H, K, M, N). The second trend is associated with evidence of relatively slow-moving to still water (Eagar 1948, 1961). These two trends in shape of shell may furthermore be distinguished within established unionid species of appropriate ecological station within a single river system (Eagar 1948, fig. 6).

Although no work on shape of shell in relation to inferred palaeoecological station has been

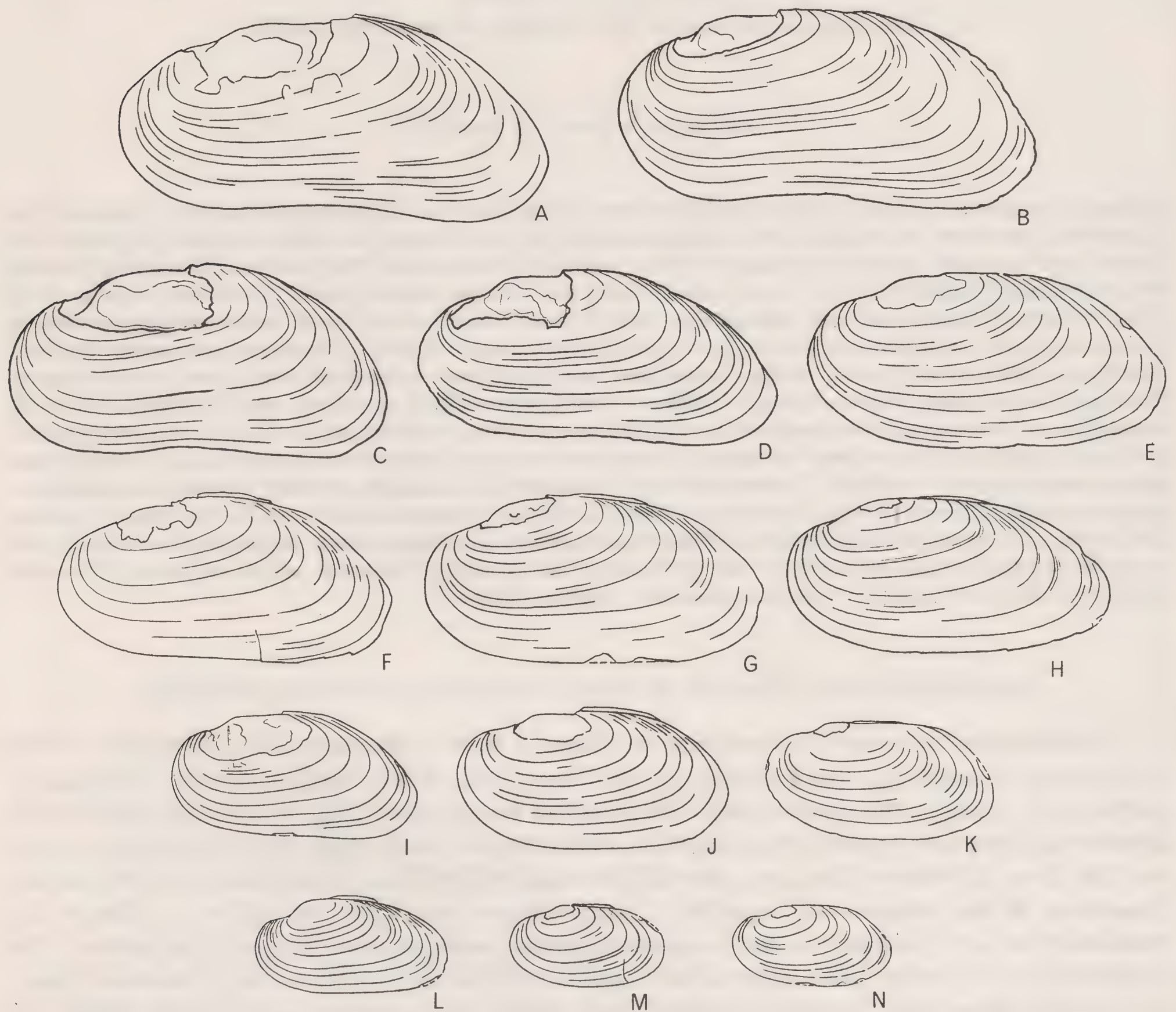


Fig. 1. *Margaritifera margaritifera* (L.); shells from various British localities now in the Manchester Museum. The lengths vary from 37 to 132 mm, measured parallel to the line of the hinge; and the specimens figured are typical of the range of shape within the size classes.

carried out on freshwater bivalve shells found in the geological record of post-Palaeozoic time, examples of the two main patterns of growth have been described in Mesozoic Unionacea (Hudson 1963; Woodward 1964) and throughout the Cenozoic Era (Haas 1969). Thus the continued representation of the 'arched dorsum' and 'curved venter' trends in smooth-shelled shallow-burrowing, non-marine bivalves of various stocks for about 300 million years adds further reason for a functional investigation of the same trends in living *Margaritifera margaritifera*.

SOME PRELIMINARY EXPERIMENTS WITH *MARGARITIFERA MARGARITIFERA*

Hypotheses concerning advantageous functional activity of *M. margaritifera* with strongly arched dorsum feeding in habitats of relatively swiftly moving water were investigated, at my suggestion, by Professor E. R. Trueman at Hull University in 1966–7. Using film techniques and recording apparatus described by Hogarth and Trueman (1967), Trueman found no differences in the shapes of the inhalent and exhalent apertural siphons in varieties with widely differing dorsal margins, for instance as shown in Figures 1 C, E. Moreover the action of the siphons, as seen with carbon colloid in the water, proved no different over the full range of variation found in living specimens from the River Lune near Caton, Lancashire (represented approximately in Fig. 1 C–N); nor did there appear to be appreciable difference in the siphonal actions of *Margaritifera* and *Anodonta* (E. R. Trueman, *pers. comm.*), although the siphons of *M. margaritifera* are pointed towards prevalent bottom currents wherever the substrate permits these orientations (Zhadin 1939).

No studies have been made of the speeds of burrowing (Burrowing Rate Index of Stanley 1970) of bivalves having dorsally arched, ventrally reflected shell profiles, as compared with varieties of the same species with the opposed 'curved venter' trend. However Trueman (1968, p. 403) has noted that in *M. margaritifera* 'The foot was never observed to extend posteriorly of the inflection ('IN' of Fig. 2) of the ventral margin of the valves at any stage of digging. In *Margaritifera* from a different habitat with more rounded ventral valve margins the foot was similarly extended, never being observed behind the mid-ventral region of the shell.' 'In the inflected forms there was also a pronounced pedal gape even when the valves were completely closed mid-ventrally, through which the outer mantle fold ('M') protruded at pedal extension. This pedal gape may possibly be associated with an extension of the foot for longer periods in those animals that live in faster waters, so as to ensure a better anchorage.' In brief, although one might reasonably expect that entry into the burrowing position (Fig. 2a) is facilitated by the reflex contour of the ventral margin, after the bivalve has ploughed the surface (Fig. 2b), such experimental evidence as exists suggests that forms with reflected ventral margins may well have been more stable in shifting sands than those with curved ones, because of an additional feature in the former, pedal gape.

Of other factors associated with these divergent morphic trends in the shape of shell of *M. margaritifera*, weight of the living bivalve appeared worthy of investigation, since it affects both the initial probing force of the foot and also the stability of the bivalve when subject to lifting forces resulting from turbulence during periods of high velocities of water, to which this shallow-burrowing species is particularly subject.

WEIGHT AND SPECIFIC GRAVITY OF THE LIVING BIVALVE IN RELATION TO AGE AND SHAPE OF SHELL

In many species of the Unionacea the relationship between weight of shell and age is linear for nearly all the life of the individual (Negus 1966, Sheldon 1967). Among this group, lives are probably longest in *M. margaritifera*, for which periods of more than 100 years have been claimed for some large individuals in Swedish streams (Hendelberg 1960). Since the annual increments to the shell, measured parallel to its surface, diminish throughout the life of each individual (Hendelberg 1960), as in other unionids (Chamberlain 1931, Negus 1966), there tends to be a general increase in the weight/volume (W/V or Specific Gravity) of the bivalve with increase in age and size, although in the collections of *M. margaritifera* herein investigated correlation has proved of a low order (Fig. 3); and in shells above the length of 70 mm no correlation has been found.

The shell itself figures importantly in any consideration of the weight and specific gravity of

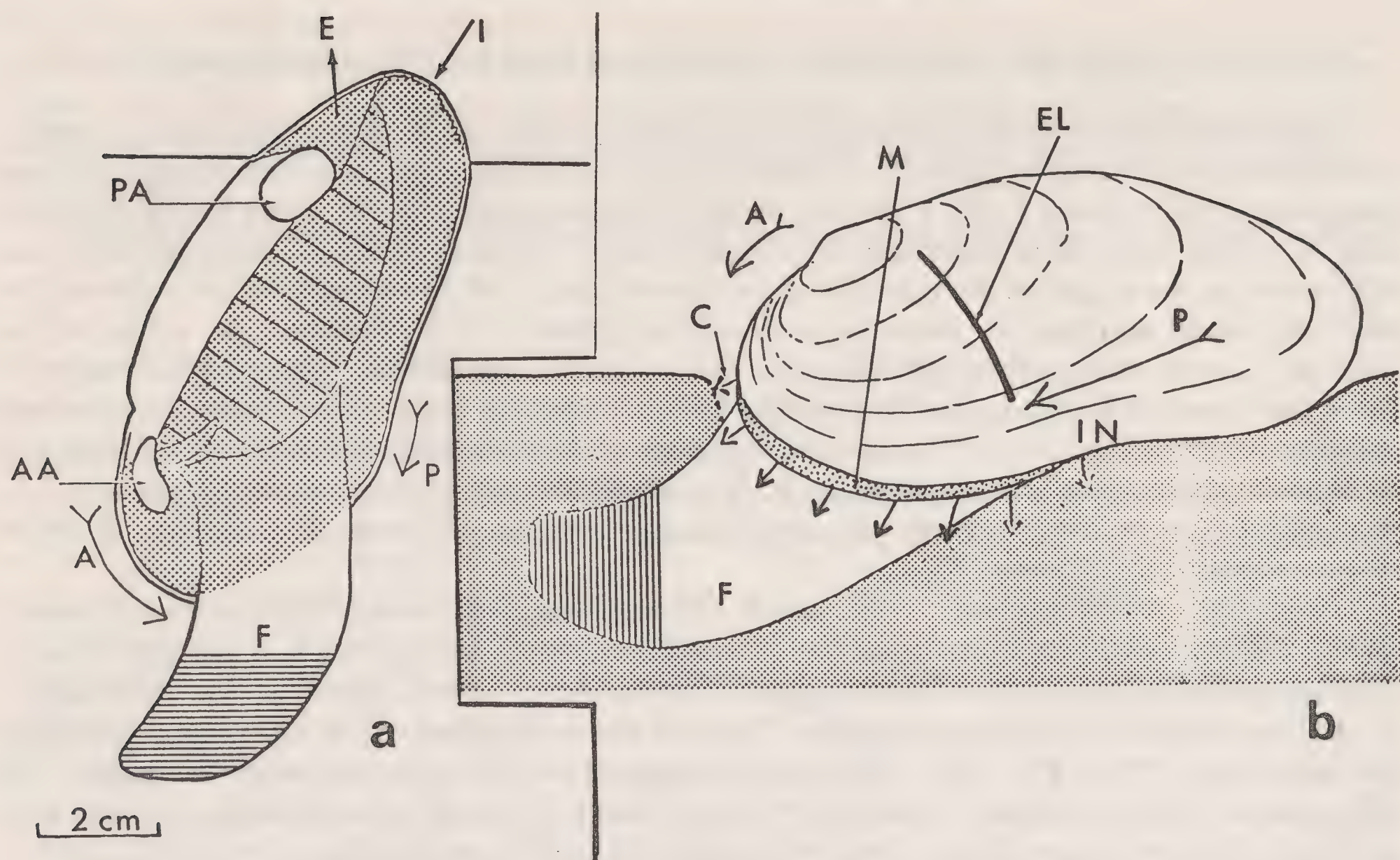


Fig. 2. Diagrams of *Margaritifera margaritifera* reconstructed from film sequences of burrowing, seen (a) when buried and (b) moving over the surface of the sand.

(a) shows a *sagittal* section with the foot (F) extended in the active digging position, the surface of the sand (horizontal line), the extent of the mantle cavity (stippled) with gills (hatched), and the inhalent (I) and exhalent (E) siphons. AA, impression of anterior adductor, PA of posterior adductor.

(b) shows the position of the foot in the sand during locomotion across the surface of the sand (stippled), water ejection currents from the mantle cavity at adduction of the valves with the siphons closed producing a cavity (C) in the sand in front of the shell and over the upper surface of the foot. IN, inflected ventral margin; M, outer folds around the pedal aperture.

In both figures the direction and relative movement of the shell by the anterior (A) and posterior (P) retraction is indicated by arrows and the region of the foot forming the pedal anchor is shown by hatching. From Trueman, 1968, by permission of the Editorial Board, *Malacologia*.

the living bivalve, since the soft tissues weigh very little more than water, having an S. G. of 1.048 (recently checked for me by Dr. W. B. Heptonstall). Thus weights in water are very closely reflected in the ratio W'/V , where W' is the weight of the dry valves plus that of the ligament. In *Margaritifera margaritifera* thickness of shell substance, and therefore weight, reaches a maximum on the dorsal margin, where the hinge plate is formed. Shell thickness tails off to a minimum on the ventral periphery. Arching of the dorsum and straightening and reflection of the ventral margin together add to that part of the shell margin which is heaviest and reduce the part which is thinnest and lightest. For bivalves of the same length therefore, the

TABLE 1

Shell form	Length in mm	Weight in g	Opening Moment of ligament
Strongly arched dorsum and reflected venter	99	35	2180 g mm
Oval shell with straight hinge line	100	28	3700 g mm

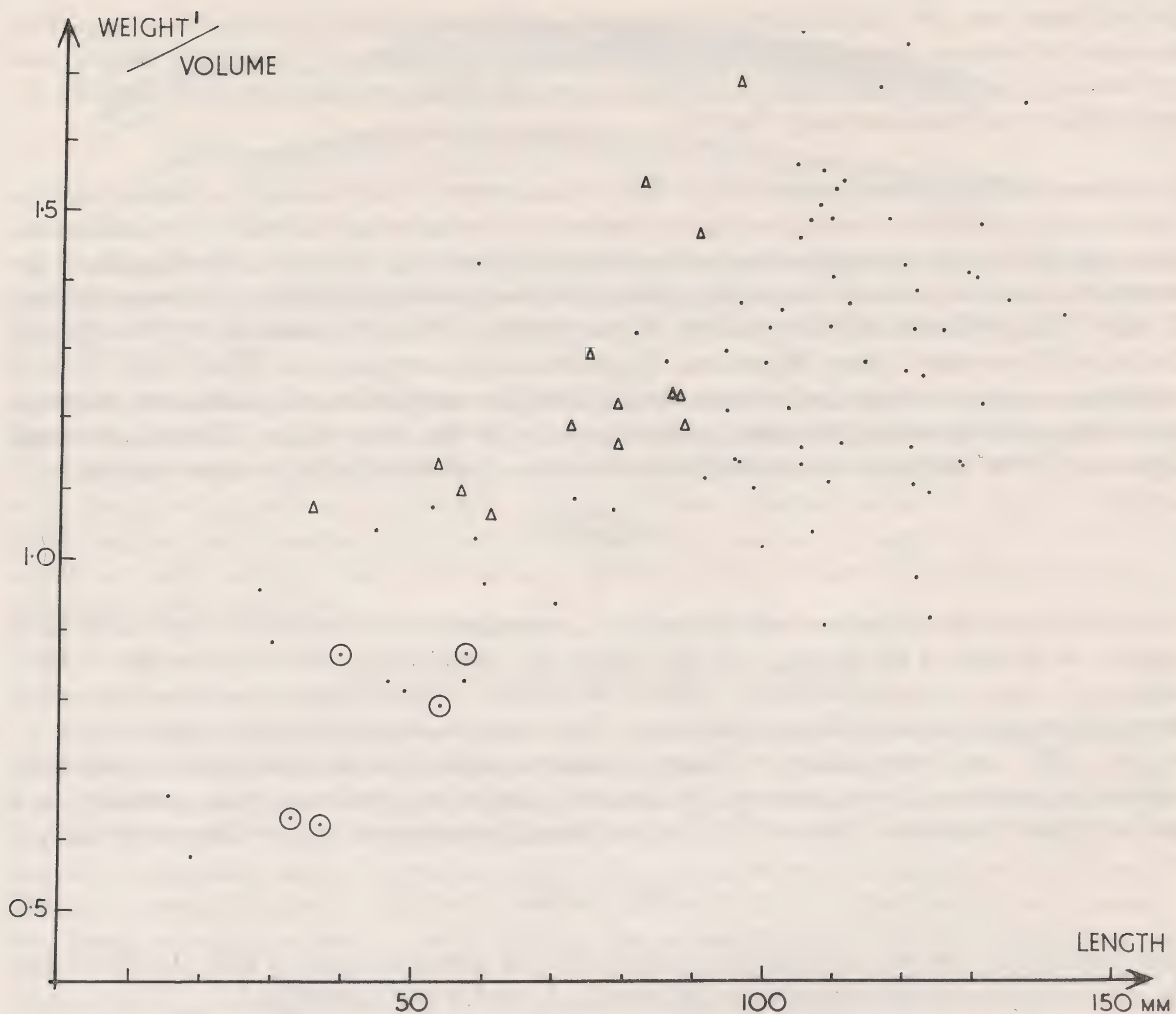


Fig. 3. Weight of dry shells (W') / calculated volume of shell (Fig. 5) plotted against shell length for British and Irish specimens of *Margaritifera margaritifera* in the collections of the Manchester, Merseyside County and Leeds Museums. Small triangles denote specimens from near Windermere (Manch. Mus.). The ringed specimens came from the Clady River, Bunbeg, west Donegal.

extreme expressions of the trends shown as Figs 1 C and E may be deduced to represent respectively the maximum and minimum weights of living specimens of the same size. This general conclusion was also suggested by the results of weighing two contrasted live specimens by E. R. Trueman (*in litt.* to me 23/4/66) as set out in Table 1 (above). Both specimens were taken from the River Lune, near Caton.

The dorsally arched bivalve had therefore the availability of 7 g or some 25% more probing force for the foot than the variety with the more oval shell, and therefore had an unquestionable advantage in the initial stage of burrowing.

SHELL VOLUMES, SPECIFIC GRAVITIES AND SHAPES

The hypothesis that degree of dorsal arching of the shell is related to the specific gravity of the living bivalve (W/V) may be investigated by direct measurement. However since it is difficult to obtain even small samples of living *Margaritifera*, especially from more than a very few localities, and since measurement of the degree of dorsal arching of a shell cannot be undertaken without killing the bivalve, it proved necessary to develop a method for calculating

shell volumes from dry valve-pairs of this species, such as are stored in museums. Valves from museum collections have the additional advantage of being in abundant supply and representative of many localities, in addition to providing internal features of the shell for the measurement of dorsal arching (Fig. 4).

Measurement and calculation of volume of shell: The measurement of shell volume by displacement of water can be made only where ligaments of preserved valve pairs have already been broken and when the infilling of valve pairs does not endanger the shells. In the older collections shells are commonly cracked, or liable to cracking around the margins during infilling. Consequently out of nearly 200 specimens of valve pairs of *M. margaritifera* in the collections of the Manchester, Leeds and Merseyside County Museums, 19 specimens only were selected, being chosen to show a maximum range in shape and volume (5 to 150 cc.) for comparison with calculated volumes. As a first approximation the closed valve has broadly the shape of an ellipsoid, although departures from this form are impossible to estimate. Accordingly the volume is given by

$$\frac{\pi LTH}{8} \quad (i)$$

where the axes of the ellipse are half the length (L, measured as the maximum length of the shell parallel to the line of the hinge), half the height (H, measured as maximum height at right angles to L within the sagittal plane), and half the obesity (T, the maximum width of the valves measured perpendicular to the sagittal plane). This formula, simplified by the removal of $\pi/2$, to give $\frac{LTH}{4}$, has been utilized in Figure 5, where calculations, plotted against values from water displacements, show a remarkable linearity, the largest deviation being provided by a shell with heavy umbonal erosion ('D'). By line-fitting the volume of *Margaritifera margaritifera* is

$$0.4375 LHT \quad (ii)$$

This empirically derived expression is independent of size and shape of shell. In fact it has proved to be the ellipsoid formed by the axes $\frac{L}{2}$, $\frac{H}{2}$ and $\frac{T}{2}$ multiplied by 1.1.

Measurement of dorsal arching of the shell: Detached valves were placed in an epidiascope which projected an image of the interior, coincident with the sagittal plane, at a magnification of about 5. All measurements were then taken after drawing directly on the enlarged image, on which fixed points could be placed at the umbo ('M') and at the termination of the ligament ('B') (Figure 4). The ratio pq/UB, where pq is the perpendicular from the point of maximum height of the dorsal margin above the line UB, is herein defined as the arching index of the shell. Due to the varying character of breaks in the ligament, it is commonly more convenient to measure the line lm of Figure 4. The ratio lm/UB is then described as the 'arching index including thickness of the ligament', where lm is the maximum height of the ligament above UB.

Results: In Figure 6 arching index of each shell has been plotted against W'/V , and it will be seen that the correlation is good ($r = 0.85$). The graph should be compared with that of Figure 3. In Figure 7 the ratio lm/UB has been plotted against W'/V of 65 specimens of *M. margaritifera* from various British and Irish localities. It will be seen that the shells included in Figure 6 have all been added to this figure (circled points) and that the correlation is significantly less good than in Figure 6, although better than that of Figure 3. For the line of Figure 6, using the method of Imbrie (1956), the equation is

$$i = 6.23 \frac{W'}{V} - 3.59 \quad (iii)$$

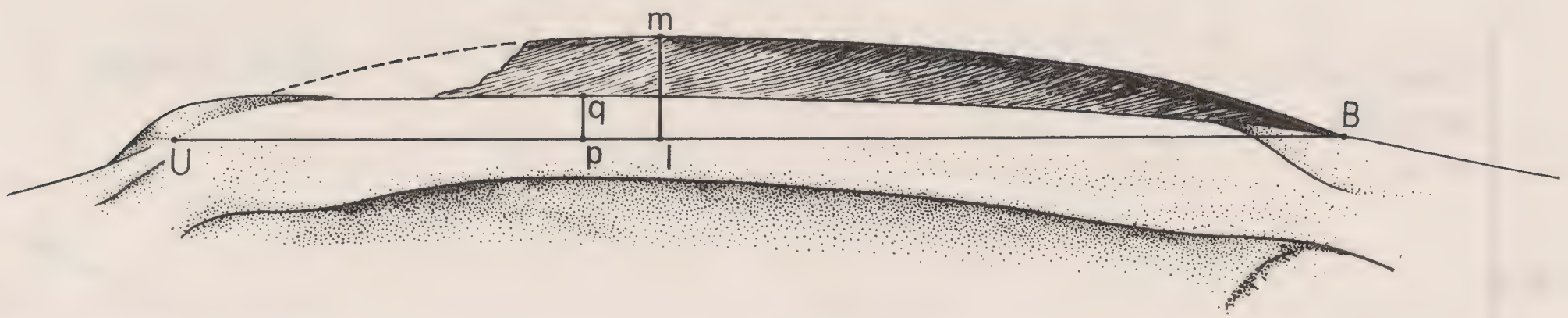


Fig. 4. Diagrammatic view of the umbo (U), hinge plate and ligament (cross hatched) of a right valve of *Margaritifera margaritifera* to show the method of measuring the arching index, pq/UB where B is the posterior limit of the external ligament. The lines of hatching of the ligament correspond approximately to lines of growth lamellae. The anterior part of the ligament is eroded.

where i is the arching index, W' is the weight in grams of the two valves and the ligament, and V is the volume of the closed valves. It may therefore be concluded that among 154 specimens of *M. margaritifera* investigated, specific gravity of the living bivalve, essentially W'/V , increased with the growing shell up to a length of about 70 mm, tending to vary a little in different localities, but that it ranged widely with shape of shell in any size group; finally that the most significant relationship is that found between specific gravity of the shell and arching index, as demonstrated in Figure 6.

THE LIGAMENT AND ITS STRENGTH

Margaritifera margaritifera is an active burrower which also moves or ploughs along the surface of the substratum, which is typically sand or gravel (Trueman 1968), and tends to find a living position such that its inhalent siphon is pointing approximately up-current, or counter-current, if the latter is developed on the bottom as a result of boulders (Zhadin 1939). In both moving horizontally and in burrowing, the bivalve is assisted by a strong ligament, although it should be stressed that when the shell is more than one third to one half buried the ligament is not strong enough to open the valves without the assistance of the foot (E. R. Trueman *pers. comm.*). Strengths of ligaments may be directly measured on recently killed bivalves (Trueman 1953). The load extension curve of *M. margaritifera* shows the typical hysteresis loop of an active burrower (Trueman *in litt.* to me 12/1/66). Ligamental strengths tend to vary with the surface area of the valve as projected on the sagittal plane (Trueman 1954). For 14 specimens from a locality near Windermere (Figure 8) the correlation between the opening moment of the valves and their surface area proved to be very good ($r = 0.93$), to give the fitted line

$$OM = 936 SA - 7419 \quad (iv)$$

where OM is the opening moment, expressed in g mm and SA is the surface area of the shell, expressed in sq cm.

Since the strength of the ligament is proportional to its thickness, and since the surface area of the shell is unrelated to its specific gravity, it will also be apparent why the correlation of arching index with thickness of the ligament (lm/UB of Fig. 7) proved less good than that of pq/UB with W'/V (Fig. 6). Of the two contrasted bivalves of Table 1, the variety with strong dorsal arching gave a comparatively weak opening moment, little more than half that of the oval variety with the straight line of hinge. Moreover it may be noted that, in Figure 4, the ligaments of the older shells tend to be eroded at the anterior end, behind the umbo, where they also split. The effect of the split in weakening the ligament is considerably accentuated by strong dorsal arching, since the hinge must operate on virtually a straight line. Thus ligaments tend to be proportionately stronger in the small- to medium-sized bivalves with relatively straight 'hinge lines', rounded ventral margins and low specific gravities, that is the 'curved venter' trend (Fig. 1, right hand side, excluding the largest shell, B).

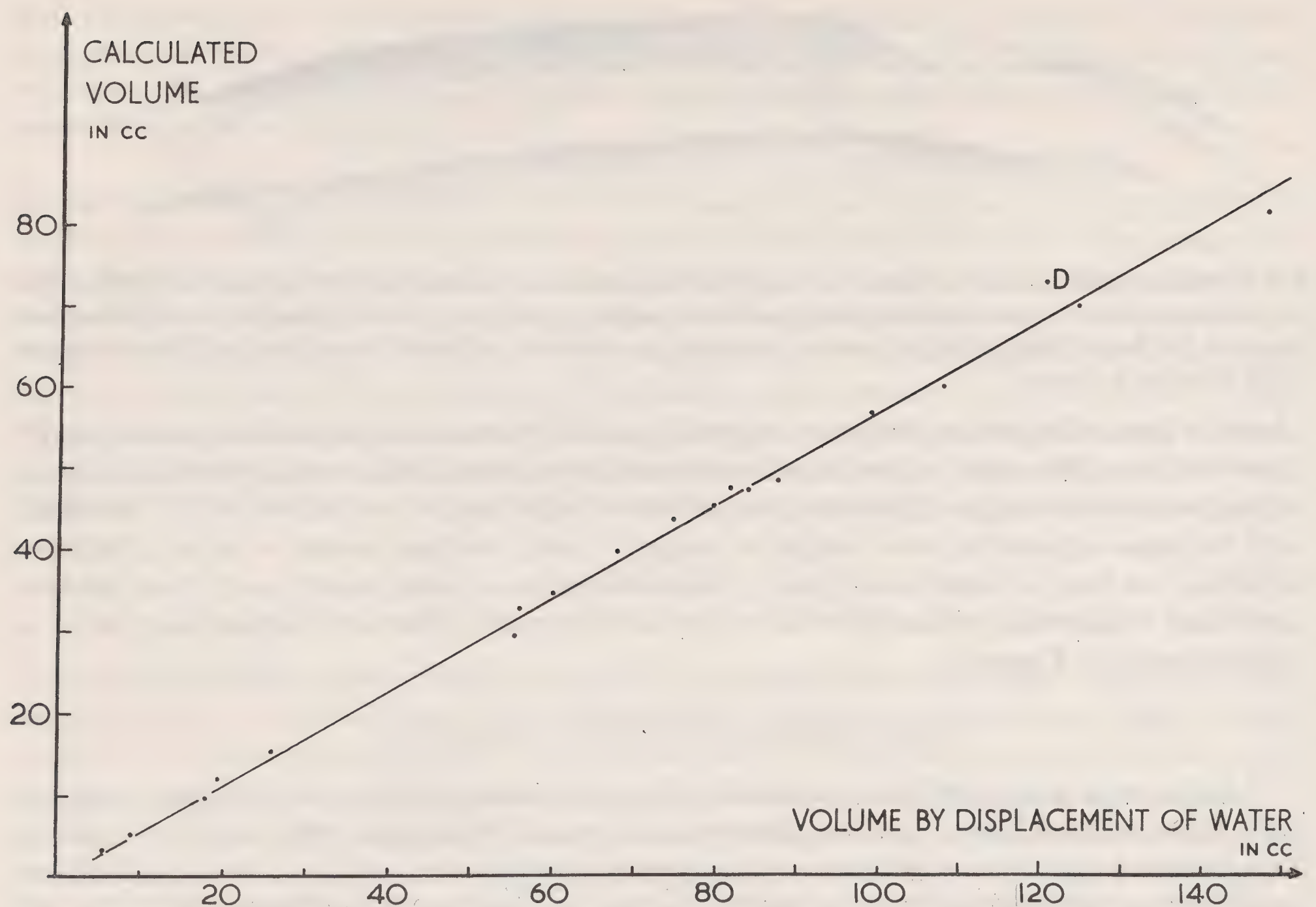


Fig. 5. Water displacement of 19 specimens of *M. margaritifera* plotted against their volumes as calculated by formula (i) (p. 212), divided by $\pi/2$. D denotes a specimen which has suffered heavy umbonal erosion.

Although the issues in this discussion have been simplified—for instance shell form results obviously from a compromise between the requirements of several functions—it is nevertheless clear that the two contrasting patterns of growth emphasized in the first section of this paper appear to have been consistently related to two main functional activities, on the one hand the provision of extra weight and probing power for the foot at the commencement of burrowing, and on the other the maintenance of ligamental strength for active surface movement. The further significance of the arching trend may be seen in studies of populations of *M. margaritifera* within stream systems.

THE WORK OF ALTNÖDER AND ITS FUNCTIONAL SIGNIFICANCE

Altnöder (1926) examined the distribution of *Margaritifera margaritifera* in a number of small streams in Germany where maximum water velocities could be assessed relatively on the basis of measured stream gradients. Mussels were found to extend upstream from the mouth of each brook to a point at which the stream gradient began to increase more steeply, above which no shells were found. The average gradient for the upstream barren sections proved to be 2.36%, whereas in the colonized stretches, which were not invariably continuous but sometimes separated by steeper barren 'pitches', the gradients averaged 1.60%. Some of the steeper 'pitches' had been modified by the building of mill ditches, through which water ran steadily at all times, and in these habitats mussels were especially abundant. It seems significant that in times of flood the associated barren 'pitches' received all the surplus water and were the sites of much turbulence, whereas commonly they were almost empty.

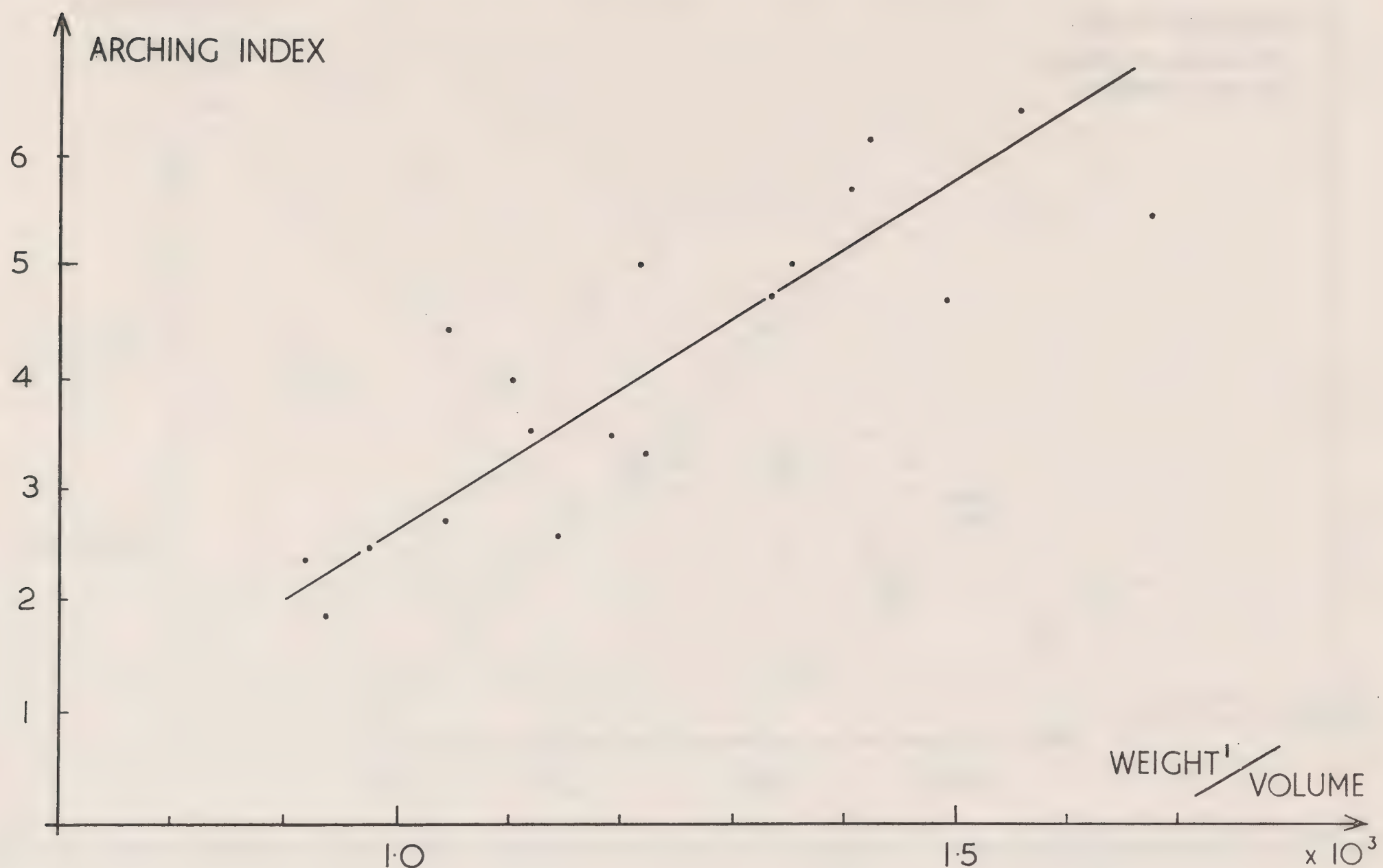


Fig. 6. Arching index plotted against specific gravity (W/V) of dry valve pairs of British and Irish specimens of *Margaritifera margaritifera* in the Manchester Museum.

Altnöder (1926) then investigated the distribution of varieties of mussels according to the gradients of the colonized sections. Shells with the strongest dorsal arching and inflection of the ventral margin (Fig. 1 A, B; Eagar 1948, fig. 5a), varieties herein recognized as the heaviest, characterized as modal forms the steepest gradients, whereas with decreasing gradient less dorsal arching was associated progressively with more rounding of the ventral margin and a slight increase in obesity as stream gradients decreased to a minimum (Eagar 1948, fig. 5b-d), as the bivalves became progressively lighter, size for size.

Within the habitat of *M. margaritifera*, as with many other freshwater bivalves, velocity of the water varies seasonally. Flooding, with abnormally high speeds and with turbulence providing an initial 'lift' for the bivalves, appears to be an occasional but critical hazard and may have been the critical factor limiting distribution on the steeper 'pitches' by removing any spat deposited irrespective of shape and size. However the transporting power of water varies very approximately with the sixth power of the velocity (see however Leopold, Wollman and Miller 1964), so that marginally increased speeds bring about considerably changed conditions at the surface of the substratum. Lighter bivalves, selectively removed in this way, become a ready prey for fish (Negus 1966). Moreover this inferred selective action of turbulence and high water velocity has received some support from experiments I undertook in flume tanks, both in the Department of Geology, Edinburgh University, where I used gelatine-filled valves of *M. margaritifera* (with S.G. approximating to that of living forms) and in the Hydraulics Laboratory of the Engineering Department of Manchester University, where the work was carried out with living bivalves. In both series of experiments medium-sized to small shells of *Margaritifera margaritifera* were placed on one or other valve, with long axes in varied positions relative to the direction of water flow, the velocity of which was increased until lift by turbulence successively removed the specimens, of which four were used of approximately the same lengths but with varied degrees of dorsal arching and straight to curved venters (Fig. 1 F-H). Lift tended to take

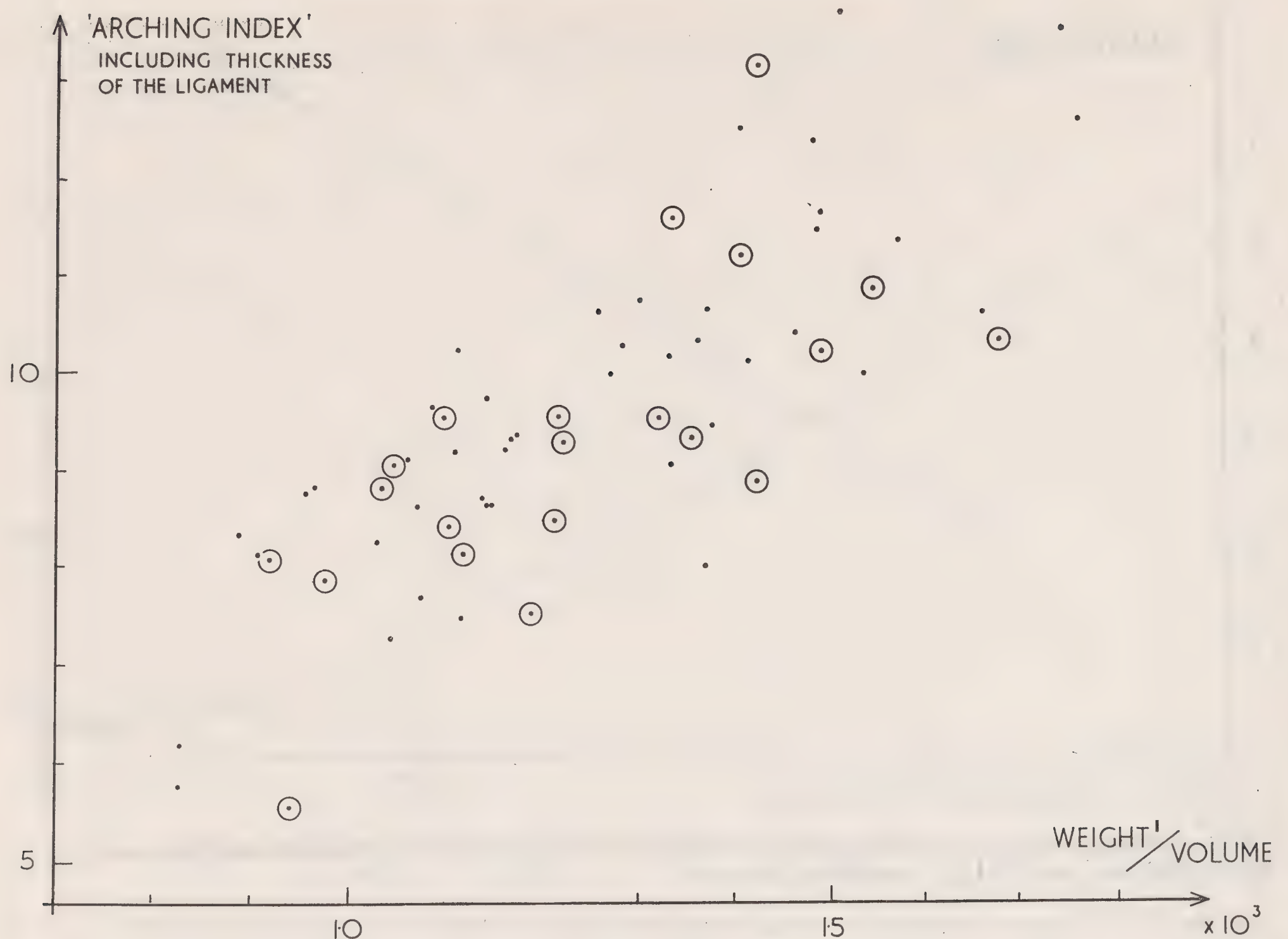


Fig. 7. The ratio lm/UB (of Fig. 4), or arching index including thickness of the ligament, plotted against weight/volume of dry valve pairs of British and Irish specimens of *M. margaritifera* from the Manchester, Merseyside County and Leeds Museums. The ringed specimens are those utilized in Fig. 6.

place in the order predicted by specific gravities, as might be expected from the work of Menard and Boucot (1951). However when shells were placed in the vertical ploughing position (Fig. 2b), irrespective of their angle to the direction of the current, turbulence usually tended to accentuate their burial in sand. It was not possible to perform experiments on floating bivalves, but this phenomenon has been commonly observed in highland streams in Sweden where dorsally arched ventrally reflected shells are well known (Hendelberg 1960). One might reasonably expect the strongly arched 'bighted' forms, with curved subparallel long axes, would tend to move more obliquely to the main current direction, and therefore to ground more quickly on the shallower margins of the stream, than the more symmetrical oval varieties.

CONCLUSIONS

In summary, the observations of Altnöder (1926), combined with the results of experimental and biometrical work outlined in this paper, strongly suggest that maximum water velocity is a critical factor in the distribution of *M. margaritifera*; that it is the primary factor controlling the distribution of modal shape of shell within populations of this species, and that it acts selectively, so that in general progressively more dorsally arched and therefore heavier varieties survive progressive increase in water velocity to the physical limits of the habitat. Whereas under more or less optimum conditions, where environments are not subject

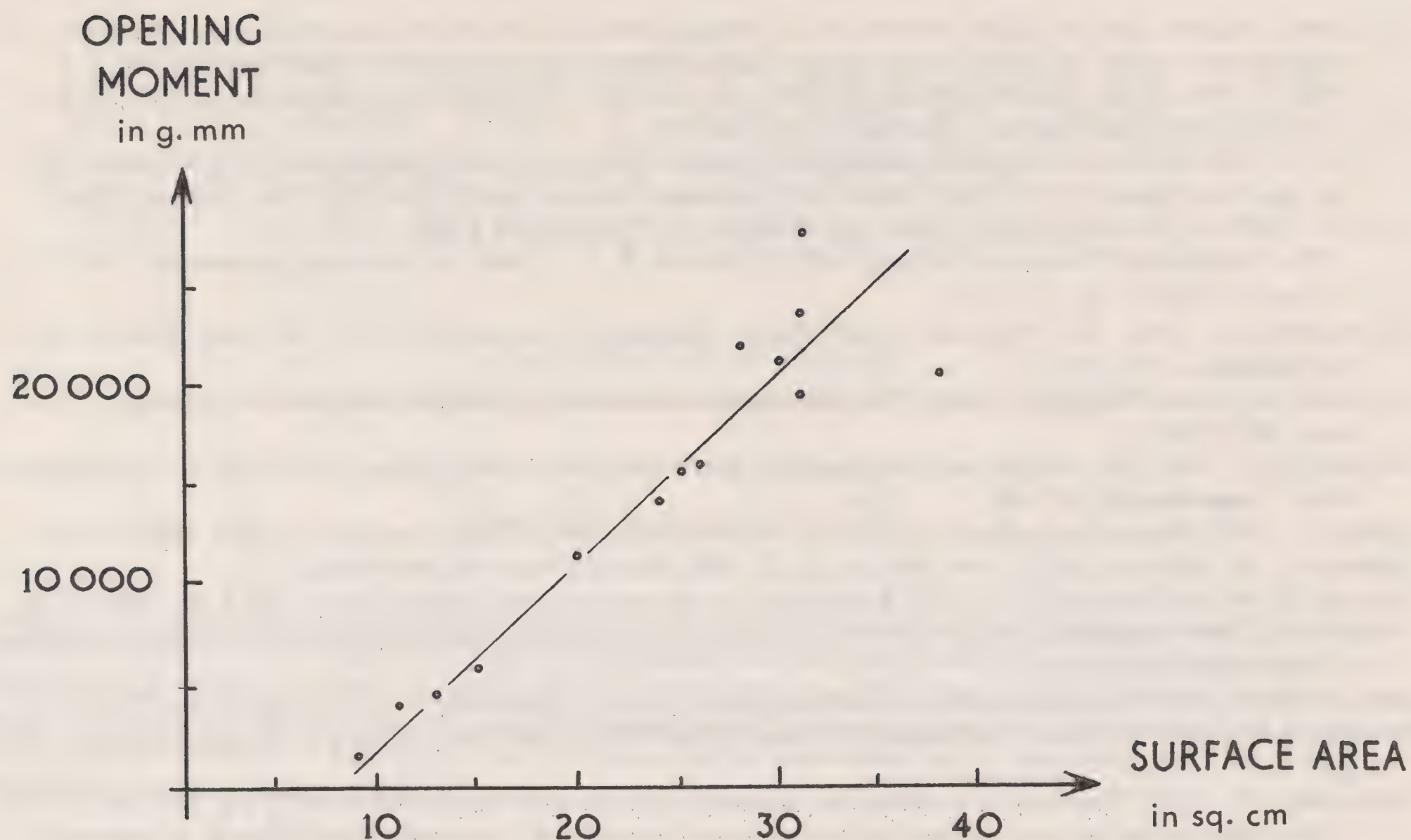


Fig. 8. Opening Moment of shell plotted against surface area for a collection of *M. margaritifera* from near Windermere.

to much turbulence, the more oval, lighter varieties have functional advantage over the heavier ones, particularly in moving over the surface of the substratum. If selection is operative, as seems likely in the case of the bivalves which differed in specific gravity as a result of different growth patterns in early and middle life stages, then the maintenance of an unusually wide range of variation in the species reflects its adaptation to an unusually wide range of environments. Moreover, in that similar divergent patterns of growth characterized various unionid stocks throughout the Cenozoic and Mesozoic Eras, and notably in the late Palaeozoic where there is evidence of the operation of the appropriate environmental factors (Eagar 1975), it seems very likely that these variational trends fulfilled broadly the same functional roles for about 300 million years.

ACKNOWLEDGMENTS

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OBSERVATIONS ON VARIATION IN THE MANTLE OF THE LAND SNAIL *MONACHA* *CANTIANA* (MONTAGU) (PULMONATA: HELICIDAE)

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(Read before the Society, 21 May 1977)

Abstract: Two distinct forms of mantle pigmentation occur in the European land snail *Monacha cantiana* (Montagu). These are figured and data are given showing the percentages of the two types of mantle from six populations in different habitats and localities in southern England. Snails with the darker speckled type of mantle were most common on nettles and in dark situations, whilst populations dominated by snails with the pale mantle form were found on grassland in open situations on downs and by the sea. The results confirm and extend earlier observations by Cain (1971) on mantle variation in the same species.

Variation in the colour of shells is fairly well documented but less has been published on the animals; these also vary in colour within a species and this can cause some confusion in the field where snails are found alive. Pigmentation of the mantle (the tissue lining the body whorl of the shell) of *Monacha cantiana* (Montagu) was noticed in the nineteenth century (Moquin-Tandon 1855) and also in descriptive work in the early part of this century (Taylor 1917 and Germain 1930). The degree of pigmentation of the mantle was also recorded for the related species *M. cartusiana* (Müller) (Gassies 1849).

More recently Cain (1971) has given a detailed description of mantle variation in *M. cantiana*, and by breeding experiments he has demonstrated that mantle colour is genetically controlled and that the dark form is dominant over the pale form. However the dark or speckled snails varied within themselves and there was a wide range in the intensity of the pattern on the mantle. Cain collected samples of *M. cantiana* from nine sites in southern England and by ranking the snails in sixteen categories of light to dark, he was able to compare the range of variation in the pigmentation of the mantle.

The present paper gives an illustration of the two types of mantle in *M. cantiana* and some further data on percentages of speckled mantles in six different populations, also in southern England.

MATERIALS AND RESULTS

Observations were made on the pigmentation of the mantle of *M. cantiana* in nettle patches at Southridge, near Reading, Berkshire (National grid reference 41/582784) – this site is described more fully elsewhere (Chatfield 1968 and 1972), behind the sea wall near Seasalter, Kent (61/063647); a horse-radish patch on the University of Reading Horticultural Station, Shinfield, Berkshire (41/737684); on chalk grassland dominated by Tor Grass – *Brachypodium pinnatum* (L.) Beauv., on a south-facing slope at the Ridgeway near Streatley, Berkshire (41/563813); a grassy bank of a dyke near the sea at Flatford Mill, Suffolk (62/077330) and sparse mixed vegetation at the base of a small cliff below the Viking ship, Pegwell Bay, Kent (61/351643). Some of these sites were investigated more than once.

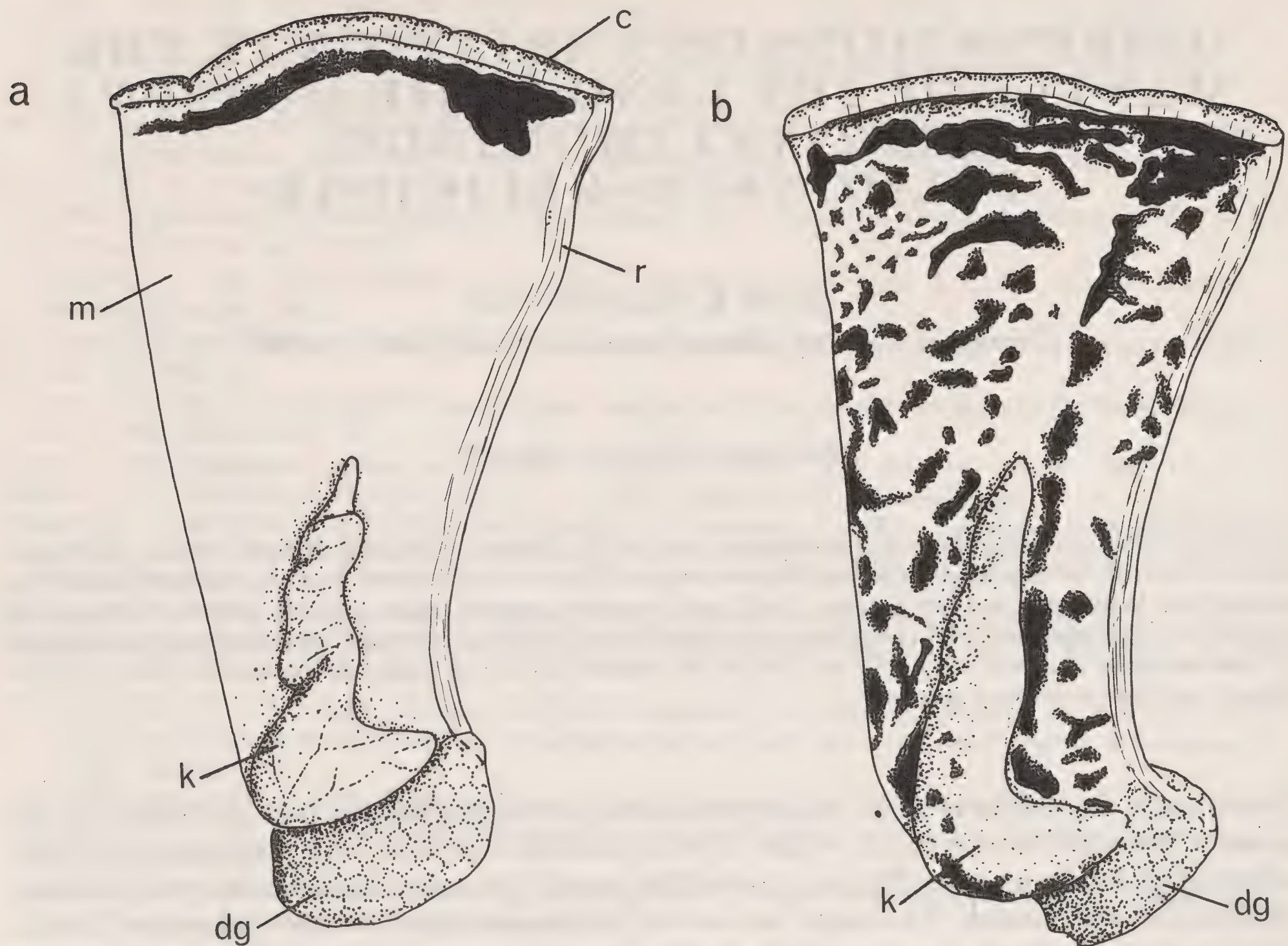


Fig. 1. Two types of mantle pigmentation in *Monacha cantiana*: (a) pale, unspeckled form from Pegwell Bay and (b) speckled form from Southridge. c, collar; dg, digestive gland; k, kidney; m, mantle; r, rectum.

In fairly young snails (before the internal shell rib has formed) the colour and pattern on the mantle is visible through the shell, and snails with heavily pigmented mantles appear dark whilst those with unspeckled mantles are light. In specimens with fairly thin shells the colour of the animal can mask the whitish colour of the shell. A more detailed view of mantle pigmentation is seen when the animal is removed from the shell and the drawings in Fig. 1 were done from specimens prepared in this way. Posterior to the mantle cavity (that is, behind the kidney), the speckled pattern can extend to the skin covering the uppermost part of the digestive gland enclosed in the spire of the shell. Although the wide range of variation in the degree of pigmentation in speckled forms was also noticed, variation within the speckled forms was not investigated in this study.

Batches of fifty or more snails were collected and they were divided into two categories: (1) pale forms in which the brown pigment was restricted to a distinct band behind the collar, broadening to a triangular patch behind the breathing pore (Fig 1a) and (2) speckled forms in which spots of pigment of different sizes were distributed over the whole of the mantle roof (Fig. 1b).

Percentages of pale and speckled snails from six populations are shown in Table 1. These results show that the speckled form of the mantle of *Monacha cantiana* was more common than the pale form in all of the samples taken from nettle patches (Southridge and Seasalter), the horse-radish plot (Shinfield) and a grassy bank with some nettles (Flatford Mill). In these populations less than 23% of the snails had pale unspeckled mantles. In contrast were the results from chalk grassland (Ridgeway) and the sea-cliff (Pegwell Bay) where the unspeckled snails (61–96%) outnumbered the speckled ones.

TABLE 1

Monacha cantiana: the percentages of speckled and unspeckled pale mantle forms from samples of snails collected in different plant communities and localities.

Habitat	Locality	Date	% speckled	% unspeckled	No. of snails	shell diameter (mm)
Nettles	1. Southridge, Berks.	22.5.1966	94.3	5.7	71	3 - 17
		20.7.1966	92.8	7.2	70	2 - 18
		27.8.1966	77.5	22.5	49	4 - 18
	2. Seasalter, Kent	15.7.1966	93.5	6.5	62	5 - 17
		24.9.1966	98.0	2.0	50	3 - 15
Horse-radish	1. Shinfield, Berks.	4.10.1965	77.7	22.3	148	5 - 16
Grassland	1. Ridgeway, Berks.	28.5.1966	10.7	89.3	56	3 - 14
		27.7.1966	38.8	61.2	54	4 - 15
	2. Flatford Mill, Suffolk	26.6.1966	92.2	7.8	90	4 - 17
Sea-cliff	1. Pegwell Bay, Kent	3.4.1966	29.6	70.4	27	6 - 16
		16.7.1966	6.0	94.0	50	4 - 18
		25.9.1966	4.0	96.0	50	2 - 17

Cain's results (1971) all showed speckled snails outnumbering the unspeckled pale ones. Although Cain did not record any populations in which snails of the pale form were more common than the speckled ones, he did show (by ranking) that in speckled snails there was a shift in the results towards lighter colouring in the samples taken on chalk grassland and the samples with a higher proportion of darker, speckled forms were mostly from deep herbage or bushes. The results in the present paper support the general trend that *M. cantiana* with speckled mantles and darker colour intensity were most common on vegetation with dark green leaves (like nettles) and dark places for the snails to retreat during daytime, whereas the pale forms were more common on grassland in light situations on open downs or by the sea.

DISCUSSION

From Cain's experiments we know that mantle pattern is inherited genetically but there is insufficient evidence to know which environmental factors control the proportions of phenotypes (the characters exhibited, regardless of the homozygous or heterozygous state of the individual) in a population. It is possible that a visual factor could operate perhaps by predation of the snails by birds. In support of this idea the author has observed birds feeding on *M. cantiana* on a pathway beside a nettle patch at Albury, Surrey (July 1964) and also the evidence of this snail on thrush anvils at the Hog's Back, Surrey (May 1966). Small mammals also feed on *M. cantiana*, but this appears to be less common than bird predation. It is possible that birds will see any snails which contrast markedly with their background and these would be more regularly culled and less likely to leave progeny than those which are better camouflaged. Further work would be necessary to investigate this.

Another possible selection factor could be the albedo (heat reflectability) of the snail. An example of pale colour in the prevention of overheating is found in desert animals (including snails) and it is possible that the relative heat absorption of the different forms of *Monacha*

cantiana could be a selective factor during some summers. This would fit the evidence where the pale form is more common in open situations with little shelter where snails would be exposed to high surface temperatures in hot summers, while pale colour would be of less significance in the shade of a nettle patch.

Cain (1971) interpreted the variation in mantle pigmentation as a polymorphism, which is the occurrence of two or more distinctive forms living together in the same habitat in such proportions that the rarest cannot be explained by genetic mutation. Polymorphisms are interesting as they show the inter-relationships between the effect of genetical inheritance and environmental pressures (natural selection) on a population. Many polymorphisms are evident as discontinuous variation and these are usually due to a major gene. There are many situations where polymorphic forms are less distinct and this is often the case where more than one gene is involved in the inheritance of a single character. These genes which give a more continuous pattern to the variation are known as polygenes.

A similar polymorphism in the mantle of another helcid snail, *Trichia striolata* (Pfeiffer) which often shares a habitat with *Monacha cantiana*, has been described by Cain (1959a) and he later performed a breeding experiment to demonstrate the inheritance of mantle colour in *Trichia* (Cain 1959b).

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Biology of opisthobranch molluscs. Volume 1. By T. E. Thompson. The Ray Society, London, 1976. 207 pp., 8 colour plates, 12 monochrome plates. Price £15.00. Obtainable from the British Museum (Natural History).

This is the first of two volumes on the British opisthobranch molluscs published by the Ray Society. Volume 1 is in two sections: the first half of the book is devoted to a comparative account of the biology of opisthobranchs and the second half is a systematic account of the opisthobranchs with shells (commonly known as Bubble Shells and Sea Hares) and the small order of the Sacoglossa. The Pyramidellomorpha (sometimes regarded as prosobranchs), Thecosomata and Gymnosomata (pteropods) are mentioned at the order level but not treated further. The remaining large order of Nudibranchia (shell-less sea-slugs) will be covered in Volume 2.

The comparative account of opisthobranchs is divided into the following chapters: Introduction, Classification and affinities, Locomotion, Food and feeding, Defence, Reproductive organs, Development, Larval biology and Life cycles. The introduction has a useful section on distinguishing opisthobranchs from other animals with which they may be confused, as some species are not instantly recognizable to the inexperienced. A good example of this is the common, but small, sacoglossan *Limapontia depressa* which looks and behaves remarkably like a flatworm. The chapter on classification starts off with some evolutionary ideas and takes the common species *Acteon tornatilis* as an example of a primitive opisthobranch. Much of the evolution of these animals is speculative as there is little fossil record and this is not covered in the text. Thence follows a general account of each of the orders (a more detailed account is given in the systematic section) and a useful feature of this chapter is the good series of drawings which give a bird's-eye view of the Opisthobranchia and illustrates the diversity of these animals. Included here is a picture of the curious bivalved gastropod (not British) which is an opisthobranch. A taxonomic list of the families in each order and examples of some of the genera follow: this list is not restricted to the British fauna, and in some of the chapters in the first half of the book, examples are given of foreign species as well as British ones. It would have been useful to have had the British examples asterisked in the list for the benefit of zoologists not familiar with opisthobranch genera.

The chapter on locomotion draws on examples from various parts of the world and describes the basic types of movement exhibited and their roles in escape and getting around. More research work appears to have been published on feeding than on other aspects of opisthobranch biology and this is understandable as they are usually specific in their food. After a general view of the various feeding patterns, the alimentary system of two sea-slugs (*Tritonia* and *Haminea*) is described in detail. The discussion in the chapter on reproductive organs concerns the problems arising in early hermaphrodite systems and the structural and behavioural separation of the different reproductive activities where both male and female systems occur in the same animal, but where cross-fertilization rather than self-fertilization takes place. At the end are descriptions of the reproductive system and its function in *Aplysia*, *Tritonia* and *Archidoris*. The remaining part of section 1 includes the development of the embryo within the egg capsule, an introduction to the variety in form of egg capsules and also the veliger stage inside the capsule (in species which have direct development) and the free-living planktonic veliger larvae of other species. The development of the larva is followed up to the stage of metamorphosis and the beginning of the life on the sea bottom. Although there were few examples to draw on in life cycle studies, this final comparative chapter points out some interesting links between the form of the life cycle and the feeding habits of the species.

The second half of the book is a systematic account of the genera and species of the Bullomorpha, Aplysiomorpha, Pleurobranchomorpha, Acochlidacea and Sacoglossa and this is the first part of the monograph of the British opisthobranchs. Throughout this section are keys to both genera and species and it is good to see more than one character listed for each entry on the key. The descriptive section on each species is full and clearly laid out under headings. The shells and animals are illustrated from several different angles and these illustrations are an invaluable aspect of the book. As the author has undertaken a considerable amount of field work, there is an emphasis on the living animal and the importance of this, rather than the shell alone, in the serious study of this group of molluscs. The heading on habitats for the various species has much interesting and useful information on most species and it also points to the many gaps in our knowledge and indicates directions for future research projects. The book is concluded with a full list of references (it is particularly useful to have the titles written out) and a systematic index. There is no subject index.

The opisthobranchs have been neglected by zoologists until recent years and part of the reason for this has been the lack of an easily obtainable and modern reference book. Alder and Hancock's monograph published in 1845-1855 has been the standard text and as this is difficult and expensive to obtain and as many new species have been added to the British fauna since then, the present book by Thompson is a welcome addition to the literature.

JUNE E. CHATFIELD

Murex Shells of the World. By G. E. Radwin and A. D'Attilio. 296 pp., 32 colour plates, 200 text figures, Stanford University Press. Price \$35.00 (approx. £20.00).

This imposing volume gets off to a good start with a useful introduction to the Muricidae, giving a general account of the animal, radula, feeding methods, reproduction and development, shell formation, habitats and distribution, behaviour and fossil record. The latter is unfortunately too abbreviated to be of any real use.

This is followed by a detailed classification, arranged strictly according to the authors' own views on the subject, which will certainly not meet with universal approval. The genera are dealt with in alphabetical order and include as well as the Muricinae, the subfamilies Ocenebrinae, Muricopsinae, Trophoninae and Typhinae.

Descriptions of the species are given in considerable detail, often accompanied with line drawings of the radula and protoconch.

The authors of this sumptuous work are unashamed 'lumpers' and whilst in some cases this is justified, some very curious synonyms are created. *Chicoreus corrugatus* (Sowerby 1841) from the Red Sea becomes a synonym of the Australian *C. denudatus* (Perry 1811), as does *C. australiensis* (A. Adams 1854), a form of *C. brunneus* (Link 1807). *C. steeriae* (Reeve 1845) and *C. thomasi* (Crosse 1872) become synonyms of *C. maurus* (Broderip 1833) and the common and widely distributed *C. torrefactus* (Sowerby 1841) which is always difficult to separate from *C. maurus*, is placed in the synonymy of *C. microphylus* (Lamarck 1816). The preoccupied *C. aculeatus* (Lamarck 1816) is renamed *artemis*, a long overdue correction.

The genus *Haustellum* Schumacher, 1817 is reduced to two species, *H. haustellum* (L. 1758) and *H. wilsoni* D'Attilio and Old 1971. No reason is given for the removal of the other species long established in the genus. *H. longicaudus* (Baker 1891) and *H. fallax* (Smith 1901) are made synonyms of *H. haustellum*, the remainder are placed in *Murex* s.s.

The genus *Hexaplex* Perry, 1811 is left with two species only, *H. chicoreum* (Gmelin 1791), the type species, and *H. stainforthi* (Reeve 1845).

In *Homalocantha* Morch 1852, the number of species is reduced to six, and many will disagree strongly with the synonyms so created, for which no explanation is offered.

Marchia Jousseaume 1880, type species *Murex clavus* Kiener 1843 (= *M. elongatus* Lightfoot 1786), is resurrected to contain a number of species previously placed in *Pterynotus* Swainson 1833, a completely unnecessary complication.

Under *Murex* s.s. the Australian *M. macgillivray* Dohrn 1862 becomes a synonym of the South African *M. brevispina* Lamarck 1822 and *M. occa* Sowerby 1834 of *M. scolopax* Dillwyn 1817. For somewhat inadequate reasons the authors have included *M. nigrispinosus* (Reeve 1845) amongst their numerous synonyms of *M. tribulus*.

The so-called 'Black Murex', from the West Coast of Central America, have all been made synonyms of *Muricanthus radix* (Gmelin 1791), the oldest name available. The authors draw attention to the high degree of polymorphism exhibited by shells of the *radix* complex and that the range of the three forms concerned overlap.

Their treatment of the genus *Phyllonotus* Swainson 1833 is almost beyond this writer's comprehension, since besides the species usually placed in this genus from the Caribbean and Panamic Provinces, they have included incredibly *M. duplex* Röding 1798 from West Africa, *M. trunculus* L. from the Mediterranean, *M. superbus* Sowerby 1889 from south east Japan and *M. laciniatus* Sowerby 1841 (synonym *M. jickelii* Tepparone-Canefri 1875) from the Philippines which they claim also occurs subtidally in Australian waters. It is strange that this species is not listed by Australian workers! It would be difficult to find a more extraordinary conglomeration of species and, as is usual in this work, no explanation whatever is offered for this arrangement. It is worth remembering that Vokes (1967 *Tulane studies in Geology* 5, no. 3) in her detailed studies of the geological history of *Phyllonotus* in the western Atlantic shows that this genus is, and always has been, confined to the New World. Perhaps the authors were unaware of the existence of this paper. One wonders.

Purpurellus Jousseaume 1888 is justifiably given generic rank, although *M. osseus* Reeve 1845 is incorrectly referred to the synonymy of *P. gambiensis* (Reeve 1845).

Under *Siratus* Jousseaume 1880, the true identity of *M. articulatus* Reeve 1845 is explained. The shells usually called *formosus* Sowerby 1841 correctly belong to *articulatus*. *S. formosus* (Sowerby 1841) (= *antillarum* Hinds 1844) is a much larger and somewhat rare deep-water species. The reference to Sowerby 1841 under *articulatus* (p. 104) should read pl. 189, fig. 69, not 169. No explanation is offered for the suggestion that *M. virgineus* Röding 1798 may be a species of *Siratus*, which is highly unlikely.

A new genus *Prototyphis* Ponder 1972, type species *M. angasi* Crosse 1863, from New Zealand is retained and the Australian *Pterochelus eos* (Hutton 1873) is made a synonym of *P. angasi*.

There are 200 excellent text figures and 32 coloured plates, all with an azure background, against which some of the small dark shells do not stand out at all clearly. On the whole the plates are good, but there are several very curious identifications. Pl. 6, fig. 4 *Chicoreus penchiniti* (Crosse 1861) is apparently *C. trivialis* (A. Adams 1854) and fig. 12 a small *C. brunneus* (Link 1807). Fig. 6 is said to be *C. florifer* (Reeve 1846), however this appears to be a perfectly good figure of *C. axicornis* var. *beta* (Reeve 1845) which is considered, probably correctly, to be a synonym of *C. banksii* (Reeve 1845). The figured shell is stated to be without data.

This writer has been unable to offer any criticism of the subfamilies Trophoninae and Typhinae, since his interests do not extend to these two groups.

Sixteen new species in seven genera are described in an appendix, all are illustrated with excellent text figures. There is an extensive and useful glossary and bibliography.

Was it too much to hope that a monographic treatment of this important family, long overdue and by no means

REVIEWS

inexpensive, would include some of the excellent features to be found in C. M. Burgess', *The Living Cowries* and Weaver and du Pont's *Living Volutes*? For example, distribution maps, location of types or type localities. Even the particulars of range and habitat given are very sketchy. Finally one looks in vain for such long established species as *Chicoreus crocatus* (Reeve 1845) and *Murex acanthostephes* Watson 1883, which are amongst some nine species of which no mention whatever is made.

T. PAIN

THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND
INCOME AND EXPENDITURE ACCOUNTS FOR THE YEAR ENDED 31st DECEMBER, 1976

	£	£	£
Publications:			
News Letter	1,081.89	
Student Papers (Reprinting nos. 6, 9, 11, 13)	41.95	
			3,674.19
Journal:			44.50
Volume 29 No. 1	1,775.44	
Volume 29 No. 2	1,107.37	
Reprints L. & F.W. List	19.20	
Cost of Atlas (Packaging and Postage)	165.59	
Printing, Stationery and Postage.	410.09	
Officers Expenses	119.10	
Subscriptions	15.00	
Advertising	26.57	
Meetings	41.20	
			704.51
Centenary Fund		134.64
Profit on sale of Greater London 6¾% Stock			16.15
Investment Income:			
General Account		579.30
Life Members Fund		164.31
Reserve and Research Fund		118.66
Transfer to Reserve and Research Fund			862.27
			118.66
			743.61
			£5,317.60

BALANCE SHEET AS AT 1st DECEMBER, 1976

	£		£		£	
Fees and Subscriptions in Advance	...		385.44	Cash at Bank: Current Account.	...	385.32
Life Membership Fund	...		1,710.00	Deposit Account.	...	1,160.34
Reserve and Research Fund	...		1,353.63	Post Office Savings		
				Bank	...	1,459.43
<i>Capital Account</i>						<u>3,005.09</u>
Balance brought Forward	...	5,914.34				
<i>Add Adjustment of Previous Years</i>						
Loss on Revaluation of Mersey				<i>Investments</i>		
Docks and Harbour Board Stock		114.60		£400 5% Treasury Stock 1986/89		344.00
				£500 5¾% Deb. Stock Mersey Docks &		
				Harbour Board 1980/82		222.29
				2,514 Units M. & G. Divident Fund		1,522.06
				£400 12¾% Loan City of Norwich		400.00
				£800 5½% Loan London County		
<i>Add Surplus for the Year</i>	...	513.80		Council		769.20
			6,542.74	1,620 Scotincome Units	...	892.95
				£875 Spillers 7% Deb. Stock 1978/83		753.82
				£500 Manchester Corporation	...	500.00
				£700 Bury 12¾% Loan.	...	700.00
				£800 15½% Treasury Stock 1998	...	768.00
				£104 Subordinated Loan Stock		
				Mersey Docks & Harbour Board		104.00
				104 10p Ordinary Shares Mersey		
				Docks & Harbour Board		10.40
						<u>6,986.72</u>
						<u>£9,991.81</u>

WM. F. EDWARDS }
L. LLOYD-EVANS }

Hon. Auditors.

1st March, 1977
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WM. F. EDWARDS }
L. LLOYD-EVANS }

Hon. Auditors.

1st March, 1977
B.C.

MARJORIE FOGAN,
Hon. Treasurer.

PROCEEDINGS OF THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND

TREASURER'S REPORT, 1976

It was unfortunately necessary for subscription rates to be raised in 1976, and receipts from Members' and Subscribers' Subscriptions are not therefore comparable with previous figures. It is an indication that Members have appreciated the necessity for the increased Annual Subscription, in that the number of Subscriptions in arrears is the lowest since 1969.

As 1976 was the Society's centenary year a special luncheon and symposium were held. After payment of all expenses there was a surplus of £134.64 in the Centenary Account, and for this the Society is chiefly indebted to the donation of £200 made by the Shell Co.

During the year the *Atlas* of the distribution of British land and fresh-water Mollusca was published, in conjunction with the Natural Environment Research Council. This has been selling well and should continue to be a source of income. Sales of other publications also show an increase.

In January 1976 £700 was invested in Bury Corporation 12 $\frac{3}{4}$ % Loan, for the benefit of the Life Members' Fund. The Society's holding in Greater London Council 6 $\frac{3}{4}$ % Loan 1976 was sold at a profit of £16.15, and was re-invested, £800 15 $\frac{1}{2}$ % Treasury Stock 1998 being purchased at £768 for the benefit of the General Fund.

16 Members and 6 Junior Members are in arrears with 1976 Subscriptions. All Members are reminded that no further publications can be sent to those whose current Annual Subscriptions remain unpaid.

MARJORIE FOGAN,
Hon. Treasurer.

REPORT OF THE COUNCIL 1976-77

Membership. It is with deep regret that the Society has to report the deaths of the following Members: Professor C. R. Boettger 1930-1976, The Rev. Canon C. T. Cribb 1910-1976, Mrs. L. L. Grantier 1958-1975, Mrs. B. J. Paton 1919-1976 and Mrs. S. C. Vowles 1974-1976. Total membership now stands at 492 Members, comprised of the following categories: Full Members—419, of whom 33 are Life Members and 4 Honorary Members; Family Members—41, of whom 5 are Family Life Members; Junior Members—32.

During the year 58 new Members were elected, only four of whom were juniors. 26 Members resigned, of whom 5 were Juniors. 6 Junior Members transferred to full Membership, one becoming a Life Member on transfer. 20 Members were removed for non-payment of subscriptions.

Subscribers. In 1976 the number of subscriptions to the *Journal of Conchology* remained static at 170. There were eight new subscriptions and eight cancellations. Subscriptions to the *Conchologists' Newsletter* also remained steady at 11.

Meetings. Six ordinary and one annual general meeting were held in the Conversazione Room at the British Museum (Natural History) as follows: 24 April 1976: Conversazione meeting and open exhibition. 15 May 1976: Open exhibition and conversazione. 2 October 1976: Lecture 'Shell stamps' by Dr. A. J. Rundle. 20 November 1976: Lecture 'Shell motifs and antiques' by Mrs. Hildegard Nash. 18 December 1976: Lecture 'Opisthobranch exploits' by Dr. T. E. Thompson. 15 January 1977: Lecture 'Shells through geological time' by Mr. G. Osborn. 19 February 1977: Lecture 'Tropical shells of the Indian Ocean' by Mr. F. M. J. Pinn. 26 March 1977: Annual general meeting: Presidential Address 'Island life—St. Helena'. In addition a joint meeting was held with the Royal Scottish Museum and the Malacological Society of London in Edinburgh on 26-27 March 1976, the subject being 'Sea slugs and land slugs'. A Centenary Luncheon was held on 24 April prior to the ordinary meeting. A joint symposium and field meeting was held at the Humphrey Rooms, Northampton with the Northampton Natural History Society as our hosts on 16-17 October 1976, with a very full and varied programme being arranged.

Field meetings. Ten field meetings were held during 1976 as follows: 28 March, Rottingdean, Sussex. 25 April, Kew, Surrey. 8-9 May, Lymington, Hants. 6 June, Northampton (joint meeting with the Northampton Natural History Society). 17-18 July, Arkengarthdale, Yorks (joint meeting with the Yorkshire Naturalists' Union). 14 August, Bollington, Cheshire. 28 August, Camber, Sussex. 26 September, Bedfordshire. 3 October, Epping Forest, Essex. 10 October, West Wittering, Sussex.

Thanks are due to the following for leading these meetings: Mrs. M. Fogan, Mrs. C. J. Pain, Miss J. T. Sawyer, Mrs. E. B. Rands, Mrs. K. A. Smythe, Dr. M. P. Kerney, Dr. A. J. Rundle, and Messrs. M. Goodchild, A. Norris and G. Osborn.

PROCEEDINGS

Publications. Two parts of the *Journal of Conchology* were issued, volume 29 parts 1 and 2. Quarterly *Conchologists' Newsletters*, an annual membership list and the programme of meetings were issued. In addition to these annual publications the Society, in collaboration with the Biological Records Centre, published the '*Atlas of the non-marine Mollusca of the British Isles*' edited on behalf of the Society by Dr. M. P. Kerney, who has been our Recorder for non-marine Mollusca since 1961 and who has had the enormous task of collecting and correlating all the many records that have gone into making this Atlas the definitive work on the distribution of British non-marine molluscs.

RECORDER'S REPORT: NON-MARINE MOLLUSCA

A. 10-KILOMETRE SQUARE MAPPING

The past year has seen the publication of the *Atlas of the non-marine Mollusca of the British Isles* (Cambridge: Institute of Terrestrial Ecology), the culmination of many years work by our society. Although I shall be glad to receive further mapping data, particularly from under-recorded areas in Ireland and Scotland (see the coverage map in the *Atlas*), general patterns of distribution are now very clear for most species and I therefore hope that our future efforts will rather be directed towards solving some of the questions which the maps raise.

A set of transparent overlays will be published by the Biological Records Centre about the middle of 1977. These will include a vice-county map.

Some errors in the *Atlas* may be corrected here:

Lymnaea glabra (map 31), delete 41/58.

Pyramidula rupestris (map 61), delete WV 27 (Channel Islands)

Vertigo alpestris (map 73), delete 35/96.

Pupilla muscorum (map 77), delete 35/21.

Zonitoides excavatus (map 117), delete 36/26.

Limax marginatus (map 129), delete 33/49.

Ponentina subvirescens (map 163), delete 10/73.

Cepaea nemoralis (map 168), delete 38/86.

Helix aspersa (map 170), delete 44/04.

Pisidium lilljeborgii (map 193). Through a computer error, the date classes on this map are pre- and post-1930, not 1950 as given on the key.

B. VICE-COUNTY RECORDS

The following new records have been verified since the last Report (*J. Conch., Lond.* 29: 121). In all cases the date of collection was 1976.

Channel Islands (0, or 113): *Hydrobia neglecta*, Vale Pond, Jersey (WV 38), R. N. Brehaut and G. E. H. Long.

Isle of Wight (10): *Leucophytia bidentata*, Ventnor (40/5878), A. Norris and A. J. Rundle; *Zenobiella subrufescens*, Chale (40/4877), R. C. Preece.

Sussex West (13): *Leucophytia bidentata*, Pagham Harbour (40/8696), R. C. Preece.

Sussex East (14): *Helix pomatia*, Litlington (51/5300), D. Whitehouse and D. T. Holyoak.

Surrey (17): *Helicodiscus singleyanus inermis*, Kew Gardens (51/1876), A. J. Rundle.

Middlesex (21): *Pisidium pseudosphaerium*, Shortwood Pond, Staines (51/0471), B. Coles.

Bedford (30): *Acicula fusca*, Old Warden (52/1344), A. Norris; *Helicodiscus singleyanus inermis*, Whipsnade (52/0018), A. J. Rundle.

Flint (51): *Limax marginatus*, Ysceiflog (33/1471), Mrs. M. Fogan.

Wigtown (74): *Oxychilus draparnaudi*, Ashfordia granulata, Drummole (25/1336), A. T. Sumner.

Ayr (75): *Hydrobia neglecta*, Ballantrae (25/0882), Mrs. M. Fogan.

Aberdeen North (93): *Anodonta anatina*, *Sphaerium corneum*, *S. lacustre*, *Pisidium amnicum*, *P. casertanum*, Loch of Strathbeg (48/0759), M. R. Young.

Clare (H 9): *Pomatias elegans*, Finavarra, Burren (M 2612), Mrs. E. Platts.

Antrim (H 39): *Boettgerilla pallens*, Parkgate (J 2387), R. Anderson.

The outstanding discovery of the past year has been the find by Mrs. Elizabeth Platts of *Pomatias elegans* living in Ireland. The colony is extensive and gives every indication of being native (for a full account see *Ir. nat. J.* 19: 10, plate 2). All previous Irish records of this species are doubtful, being mostly based on shells picked up on beaches; nevertheless a few of the old reports perhaps now merit a closer investigation, for example one from Youghal, Co. Cork (*Ann. Mag. Nat. Hist.* 6 (1840): 116).

Helicodiscus singleyanus inermis, first discovered in Britain in 1975 (*J. Conch., Lond.* 29: 121), has been detected in two further localities, in Bedfordshire and Surrey. At both places Dr. Rundle recovered dead shells from soil siftings, collected in waste ground at the foot of walls. The suggestion frequently made that this somewhat mysterious snail might be subterranean has recently been confirmed by the discovery in south Holland of examples living in earthworm burrows, between 50 and 125 cm from the surface (*Natuurh. Maandblad.* 65: 192). For a full account of the British discoveries see *J. Conch., Lond.* 29: 137.

There are no certain previous records for the Roman Snail (*Helix pomatia*) in Sussex, though it is locally common on the North Downs in Surrey and Kent. Mr. Holyoak reports that the Litlington colony is in a remote spot and that recent introduction seems unlikely. The habitat is blackthorn scrub on chalk.

Boettgerilla pallens has been found at a second Irish site, about 40 kilometres from the original locality on the shore of Strangford Lough (*J. Conch., Lond.* 28: 207). The habitat is an abandoned quarry, obviously only recently colonized.

Anodonta anatina, *Sphaerium lacustre* and *Pisidium amnicum* from the Loch of Strathbeg are considerable extensions to known ranges, *P. amnicum* in particular here being over 150 kilometres north of its previously most northerly known British occurrence in the midland valley of Scotland. It is interesting to note that *A. anatina* was reported from the immediate area by William Macgillivray in 1843 (*A history of the molluscos animals of the counties of Aberdeen, Kincardine, and Banff.* 241).

M. P. KERNEY

RECORDER'S REPORT: MARINE MOLLUSCA

A. RECORDING

The system of Area Representatives was founded on the belief that each Area Representative would receive, and coordinate, a steady supply of records from recorders. But the chosen Area Representatives were those members already active in recording; consequently the people most likely to produce records were the Area Representatives themselves. Some Area Representatives regret this but the fact remains that, with a few exceptions, the majority of Area Representatives are themselves doing much of the field work in collaboration with a few dedicated recorders. If any one would like to help with the marine census please contact your nearest Area Representative, addresses of whom will be circulated with the next Newsletter.

Area Representatives with badly under-recorded 10 km squares can supply me with details and I will publish them in the Newsletter.

B. AREA REPRESENTATIVES

The following changes have taken place:

- a) Dr. P. Lingwood has taken over from Mrs. N. McMillan in Area 24 Liverpool Bay.
- b) Dr. J. Chatfield has taken over Area 22 Cardigan Bay from Mrs. J. L. Charlish and Mrs. A. M. Brockbank.
- c) Dr. Joan Llewellyn Jones has taken over, as a temporary measure, Area 12 Wash from Mr. J. Llewellyn Jones.
- d) I have removed the Irish part of Area 29 and put it in the care of Mr. M. Briscoe of Larne, Antrim. The new subarea will be known as 29a Antrim. It is bounded, on the west, by Area 33; comprises the north coast of Ireland to Area 28; includes, along its eastern margin the 10 km squares 15/40. 70,80,90 and 16/40. 00,10,20; and, along its northern margin, the squares 06/50,60,70,80,90. 20 and 15/00,10,20,30,40. 20.

Reports were received from 15 areas of which 4 had nothing new to report. The rest reported a total of 41 new records and 56 upgraded records. Many area master cards are beginning to look very 'healthy'. Area 16, Portland, has a total of 404 records of which 236 are post 1950 live records. Area 18 has 480 records of which 281 are post 1950 live records.

C. MARINE RECORDER

My term as Acting Marine Recorder during 1976 was only nominal until November, since when I have attempted to compensate for my unavoidable neglect by starting a series of articles in the Conchologists' Newsletter designed to give the marine census some direction, cohesion, policy, uniformity of procedure, and I hope, a stimulus. I have started to transfer area master cards onto A4-sized cards so that they can be either published or, at least, xeroxed for general distribution. Some Area Representatives have begun to send me 10 km master cards so that, to date, I now hold 10 km records for Areas 2, 11, 14, 15, and 29.

PROCEEDINGS

During May 1976 the Conchological Society had a very successful trip to Ireland, organized by members of Ulster Museum and Elizabeth Platts. The trip was centred on Dunglow in Donegal and localities were visited from Donegal in the south to Ballyness in the north. Dr. Garrad's work, together with the results of this trip, gave Area 34, Donegal Bay, last year's most spectacular advance. A return trip to this delightful country is to be expected, perhaps in 1978.

C. P. PALMER

INSTRUCTIONS TO AUTHORS

Authors of papers submitted for publication in the *Journal of Conchology* are urged to pay careful attention to the following notes. Any author who has difficulty in complying with these requests, or has queries concerning manuscripts, should consult the Hon. Editor **before** submitting a manuscript.

1. Manuscripts should be sent to the Publications Committee, c/o Dr. M. P. Kerney, Dept. of Geology, Imperial College, London, SW7 2AZ.

2. **Two** copies of all text and illustrations should be submitted. (A few years ago the entire copy for one issue of the *Journal* was lost in a mail robbery!). Authors are strongly recommended to retain a further copy for proof correction.

3. The text should be **fully revised**, typed **double spaced**, with wide margins (at least 1 inch), pages numbered consecutively and should conform in style to recent issues of the *Journal*. Titles should be concise and apposite, address(es) of author(s) should follow the title. Linear measures and weights should be metric and authorities for specific names should be given when first mentioned. Location of voucher material should be stated wherever possible. A brief, but informative, abstract should precede the main text.

4. Originals of text-figures should be $1\frac{1}{2}$ –2 times the final size but should not exceed 25 by 36 cm. They should be drawn in Indian ink on clean ground, numbered consecutively, and referred to in the text as “Fig. 1” etc. Authors are strongly urged to construct text-figures so as to make full use of the page width and to submit a copy reduced to final (published) size wherever possible. Lettering should be legible and not less than 1 mm high after reduction.

5. Plates should only be used when essential and **must** not exceed 19.5 by 15 cm. They should utilise quality prints showing fine detail and moderate contrast. As far as possible prints on one plate should be matched for contrast and brightness. Authors are urged to make fullest use of plate space due to the high cost of printing plates. In the text the explanations of text-figures and plates should follow the references.

6. Tables should be concise, fit into the text and table headings should be self explanatory wherever possible. Tables are not printed “boxed”.

7. All papers referred to in the text (including synonymy lists) should be listed alphabetically by author's surnames at the end of the text under “References”. For books give author's name, initials, date, full title, pages, plates and place of publication.

e.g.

ELLIS, A. E. 1926. *British snails. A guide to the non-marine Gastropoda of Great Britain and Ireland, Pliocene to Recent.* 275 pp., 14 pls., Oxford.

BROWN, P. and STRATTON, G. B. (Editors). 1965. *World list of scientific periodicals published in the years 1900–1960.* (4th Ed.) 3 vols. London.

For periodicals give full title of the article, title of the periodical abbreviated according to the World List (4th Ed.), volume number, page numbers and plates.

e.g.

WOODWARD, F. R. 1965. Monograph of the British Lower Tertiary Unionidae, with descriptions of three new species. *J. Conch., Lond.* **25**: 316–330, pls. 22–27.

GOULD, S. J. 1969. An evolutionary microcosm: Pleistocene and Recent history of the land snail *P. (Poecilozonites)* in Bermuda. *Bull. Mus. comp. Zool. Harv.* **138**: 407–532, 5 pls.

8. Authors may obtain copies of all papers (other than brief notes) at cost price if ordered from printers (address: Messrs. Willmer Brothers Ltd., 62–68 Chester Street, Birkenhead, England) when galley proofs are returned.

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CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND

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CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND

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Meetings are held at the British Museum (Natural History) at 2.30 p.m., usually on the third Saturday of each month from October to May. Field Meetings are held in the summer.

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NOTICE

Payment by Overseas Members

Overseas members are reminded that all monies due to the Society are payable in sterling.

ISLAND LIFE: ST. HELENA

T. E. CROWLEY

The Cottage, Church Street, Bampton, Oxford

(Presidential address, delivered 26 March 1977)

Throughout his working life Darwin had a particular interest in islands, both their formation and the life which they support. It is perhaps not impossible that the whole concept of the Origin of Species occurred to him as a result of his study of island life; we know a great deal about his early visit to the Galapagos Islands for instance, and his fascination for what he found there.

Darwin had not gone very far before he discovered that he was not alone in studying islands as signposts to the mysteries of life, and if he had never existed, the theory of the Origin of Species by natural selection would have been put before the World anyway, in the 1860s, by Alfred Russell Wallace. It was he who pointed out in detail the enormous disparity between the distribution of animals and the distribution of land on the Earth's surface, and the formulation of Wallace's 'Realms' originated the new science of Zoogeography.

Wallace (1880) realised of course, that many islands have faunal assemblages so peculiar that they had to be excluded from his proposed realms, and it was assumed that these communities represented preserved relics of earlier, geological realms. As usual, of course, things in nature are vastly more complex than that, but his pioneer work undoubtedly formed an adequate basis for further research.

Islands in some ways simplify the problems of botany and zoology, since they provide a restricted area, boundaries are sharply defined, the zoological and geographical boundaries coincide, the taxa are limited, while the influences of climate and habitat on those taxa are usually comparatively simple, uniform and evident.

There are two kinds of island, the oceanic and the continental: that is, the created or the separated. The zoological difference is fundamental, since a separated island starts with a more or less full quota of life similar to that of the nearby mainland, even though the two assemblages may later be modified in diverging ways. This country of Great Britain, separated from the European mainland only yesterday, geologically speaking, has not yet had time to develop any modifications to its fauna: it has, for instance, no endemic mollusc, and with the paramount disturbing influence of mankind, such modifications as may occur in the distant future may well be atypical. Older islands round our shores however, show the beginning of modifications: it is possible to distinguish the voles from a number of different Hebridean islands, St. Kilda is famous for a modified variety of the wren; and there is always the arguable Manx cat. The Lusitanian elements in the West of Ireland arrived there, probably sea borne from Portugal, because the older island fauna, with its curious imbalance, offered niches to fill.

New species can be formed only where and when there is room for them, and a balance is never struck, even in the absence of mankind. Adaptation to circumstances can never be perfect, since the circumstances themselves (e.g. the climate) keep changing. It is however likely that circumstances change less on islands, both in respect of habitats and the absence of invaders, either predatory or competitive: in such cases there is a risk that adaptation will become over-specialization.

Conversely, the main reason for extinction in past ages is pressure of other species. In the case of islands which start with a more or less balanced fauna this pressure will be minimal, and there will be a tendency to preserve recessive species; with isolated islands, however, which start without any form of life at all, we are mainly concerned with the capricious results of the powers of dispersal of species. One important point here is that there is nearly always a lack of dominants, and since the accretion of species is slow, depending on the isolation of the island, there are usually more ecological niches available than there are animals to fill them. This brings about over-specialization and a lack of competition; no animal struggles to master as varied an environment as possible and each new species arriving on the island, if it does not die out, finds an unoccupied niche which it can make its own, snuggles down into it and becomes highly dependent on it. In other words, it over-specializes, becomes enervated, and increasingly vulnerable.

Isolated or oceanic islands are of two types, the volcanic and the coralline. (The only exception, the Seychelles, are of granite). Darwin noted that no oceanic island contains indigenous Mammalia or Amphibia.

The volcanic island of St. Helena is almost the perfect example of its type, combining as it does, extreme isolation with a rich indigenous fauna and flora. It is situated 1100 miles (1700 km) from Africa, 1800 miles (2880 km) from America, and the sea all round it ranges down to over 3000 fathoms (5540 m). It is, in fact, a submarine volcano whose crater just breaks the surface.

It measures ten miles by eight and is entirely volcanic, being composed of ancient basalts and lavas. It is mountainous to a degree, rugged with enormous precipices and rises to a great crater four miles across at a height above sea level of 2700 ft (830 m), besides which most of the island consists of a windswept plateau 1500 ft (460 m) or more in altitude. Shallow seas, representing the process of denudation, extend to only $1\frac{1}{2}$ miles round the coast, ending in a submarine cliff. Marine Mollusca are scanty, both in species and individuals, and show few unexpected characteristics, although there is an endemic limpet.

When St. Helena was first discovered by the Portuguese in 1501 it was densely covered with luxuriant forests of indigenous vegetation which gave cover, repelled invading species, prevented erosion and protected the fauna, but the ecology of the island was doomed as early as 1513 when the Portuguese introduced goats: these above all animals are the great enemies of trees.

The East India Company took possession in 1651 and it was not before 1700 that there appeared any recorded concern about the rapidly diminishing forests. The indigenous redwood and ebony at this time were used only for tanning, that is to say the bark was stripped from the trees and removed, leaving the trees to die where they stood. The Governor of the day seems to have realised that this situation was less than satisfactory and recommended to the E.I.C. that the vast flocks of wild goats should be destroyed, as they entirely prevented the regeneration of native trees, and the island was beginning to suffer drought. The reply he received instructed him to encourage the goats as being more valuable than the trees. Thus passed St. Helena's last chance. By 1810 the forests were all gone and the island was *importing* fuel at a cost of nearly £3000 p.a. European, Australian, American and African plants were being imported and naturalized, many ran wild and managed to eliminate the remainder of the native flora. Much of the island is now covered with a dense and dreary blanket of New Zealand flax.

The extirpation of a highly peculiar flora must have resulted in the destruction of a great many of the lower animals, and most of the endemics had died out by the time anyone got round to studying them. Darwin visited about 1835 and picked up a number of snails which were described by Sowerby (1844) in an appendix to Darwin's study on Volcanic Islands (Darwin 1844). E. L. Layard spent a short while on the island in 1850 and J. H. Blofeld in 1852; the shells they collected were described by Benson (1856) and by Blofeld and Forbes (1852), respectively. After that, twenty years elapsed before the fauna received any detailed attention. John Charles

Mellis in his book 'St. Helena: a Physical, Historical and Topographical Description of the Island' 1875, deals fairly thoroughly with the Mollusca, many of which he found subfossil only, but their variability was such that he found difficulty in clearly differentiating between the taxa involved, and described as species a number of individual variations. He was followed by T. Vernon Wollaston, who spent six months in 1875–6 surveying the insects and molluscs, and published one book on each. As regards the former, in spite of undoubted losses in the preceding two centuries, he reported 129 aboriginal species representing 39 indigenous genera, two thirds of which were Rhyncophora (weevils) not noticeably related to any from elsewhere. He also found 74 common introduced beetles. As regards the Mollusca he reported (Wollaston 1878) 29 species (perpetuating some of Mellis's names), of which seven were introductions and two others closely related to snails living elsewhere—that is, the influence of isolation in their case had not been in operation for very long. Of the other twenty, thirteen were extinct and found only semi-fossil in old soil, these endemics had no clear affinities anywhere in the World and were an indication of a very ancient immigration in Miocene, possibly even Eocene times. He correctly reported the complete absence of any indigenous freshwater flora or fauna.

Captain Turton did some even more thorough collecting, and a number of his species, new to science, were described by Edgar Smith in 1892. Turton was unable to find some of the species previously described. Work on the island's Mollusca this century, apart from a note by Ancey (1901) has been mainly in the hands of Pilsbry (1892, 1920) and Germain (1929). In 1965 and 1967 successive expeditions to St. Helena were organized by the Musée Royal de l'Afrique Centrale, Tervuren, (MRAC) Belgium to carry out a plenary survey of the life to be found on the island; all the landshells then collected came to Mr. Pain and myself for evaluation, and it is with Mr. Pain's valued assent that I make the following comments on our joint conclusions.

First, the introduced species are as follows:~

Carychium tridentatum. Found for the first time by the 1967 expedition, and in one spot only. Evidently quite a new arrival.

Cochlicopa lubrica on the other hand was found by Loveridge in 1958: now common in low lying areas.

Vertigo pygmaea is a slightly later introduction than the last: Loveridge, 1963 (Reported to MRAC).

Lauria cylindracea. Reported by Benson (1856) and now common on cultivated land.

Vallonia excentrica. Literature records *V. pulchella* only, but Loveridge and the Tervuren teams found only *excentrica*, and this well established in various parts.

Ceciloides acicula. Found at Jamestown by Layard in 1850 and for which Benson (1856) gave the singularly inappropriate name of *Achatina veru* on the basis of one specimen. MRAC team found several.

Opeas pumilum. Also reported by Layard, probably imported with West Indian plants. Now well established.

Helix aspersa. Well established by the 1870s and flourishing ever since.

Oxychilus cellarius, *O. alliarius* and *Euconulus fulvus* similarly reported from the 1870s and still doing well.

Pleuropunctum pusillum was listed by Wollaston, 1878 from various places, but has not been found by any recent searchers.

Arion hortensis. Found commonly in many places by the MRAC teams, although not previously noted.

Arion ater-rufus. A single specimen found in 1967.

Milax gagates. Introduced with plants (Mellis and Wollaston); not found recently. Never dissected, so it may be a misidentification.

Deroceras reticulatum. Reported by Germain 1929 and still to be found.

The position as regards the endemic snails is obscure and must now remain so permanently.

The very deposits in which the 19th Century conchologists found the subfossil specimens have vanished—washed away into the sea, and although we have in many cases precisely described localities, the Belgian expeditions were able to find little or nothing. The shining exception is *Succinea sanctaehelenae* (Lesson), a variable species which still flourishes. Given many names in the past, it is now established as a single species although it varies greatly in shape from something resembling a *Catinella arenaria* to a close approximation to *Succinea putris*. It is abundant in the island, in dry as well as damp places, and dissection, kindly carried out for us by Dr. Lloyd-Evans, indicated no near relationship to any known European, African or Australian species.

Of the rest, we have: *Nesopupa (Helenopupa) turtoni* (Smith), of the Vertiginidae, a 3 mm shell, subrimate and with a small, irregularly quadrate aperture bearing six internal denticles. Turton collected it from Sugarloaf Quarry and it has not been found since. *Campolaemus perexilis* (Smith), also ascribed to the Vertiginidae, it is a $1\frac{1}{2}$ mm \times $1\frac{1}{2}$ mm monstrosity with a highly distorted body-whorl turned back so that the figure of eight shaped aperture points towards the apex, giving it somewhat the appearance of an *Opisthostoma*. The genus is monospecific, and the connection with any other is so remote as to be invisible. The species has not been found since Turton's day.

The Belgian expedition found numerous badly worn specimens of a *Gastrocopta* (Pupillidae) of indeterminate species but which cannot be attributed to anything described hitherto, at least in Europe. Nothing like it had previously been reported from St. Helena either, and we have declined to describe it as new owing to the worn and fragmentary condition of the remains; it seems to measure about $2\frac{1}{2}$ mm long and has three denticles.

Another somewhat unsatisfactory inhabitant known so far as '*Pupa*' *obliquicostata* Smith was picked up by Turton at the Sugarloaf Quarry. It is 2 mm long and its affinities remain doubtful; Pilsbry guessed it to be a *Truncatellina* with a second choice of *Negulus*. Our criticism of his opinions is purely destructive.

Chilonopsis is the name of a genus in the Subulinidae; many species have been described from St. Helena but we believe there are eight which can be distinguished, together with a subspecies. Pilsbry (1904) reported that two of these species were thought to be lingering on in very restricted and inaccessible areas but the entire genus is now undoubtedly extinct. Pilsbry was able to establish the affinities of *Chilonopsis* by obtaining by a happy chance the jaw and radula in a dry shell. Turton found abundant subfossil material in old deposits, all now washed away. *C. nonpariel* (Perry), with its apparently very constant subspecies *darwinianus* (Forbes), is large—up to 50 mm in length, and markedly philogerontic. It was last seen alive in or about 1864. *C. subtruncatus* (Smith), *C. melanioides* (Wollaston), *C. exulatus* ('Benson' Reeve), *C. turtoni* (Smith), *C. helenae* (Quoy and Gaimard) and *C. blofeldi* (Forbes) were all collected by Turton, in some cases by others before him, and in some cases from abundant material. The differences between them are as well demonstrated by Smith's excellent figures as by their descriptions. *C. supplicatus* (Sowerby) was collected by Darwin. No trace of any of these has been found this century.

Lastly, there is a group of Endodontids which are practically unsortable under the generic name *Helenoconcha* Pilsbry. Eight species have been described but most of them appear to be mere variants or juveniles of *H. bilammellata* (Sowerby) or *H. polyodon* (Sowerby). One other type seems consistently to occur without denticles, and again, many species of it have been described. Pilsbry gave it the generic name of *Pseudohelenoconcha* and we would maintain one species only, *spurca* (Sowerby). All known specimens were collected ninety years ago or more.

The endemic Mollusca are held to represent a South African and a European element; the latter is evidently extremely ancient and bears only a remote generic or familiar affiliation. Whatever facilitated the transfer of fauna from Europe to St. Helena ceased at latest in Miocene times. On the other hand, the possibility of life being transferred to the island from southern Africa may be said to continue to this day in view of the direction of the prevailing trade winds and currents, and the existence of the stepping stone of Ascension Island, which used to be considerably larger than now, as evidenced by its considerable continental shelf. Ascension

Island itself, is tragically unable to provide us with any clues about life on St. Helena because of comparatively recent volcanic eruptions which destroyed all life.

In Tertiary times a semitropical climate extended into northern Europe, and the recession of the icecap in those days undoubtedly brought prevailing north-eastern winds and a southern temperate region of storms involving the area of St. Helena: thus the likelihood of infection would then have been from Europe. However, these peculiar forms on the island may have been the descendants of widespread Miocene types which had died out elsewhere a long time ago. They seem to have been characteristic of old island faunas—that is, a small number of original generic types (in the case of the Mollusca, about six), some of which have become modified to fill niches more usually occupied by the species of numerous genera. Such modifications, lacking competition, then became gerontic, and the ageing of the species continues at an accelerating rate, with the production of variously and irregularly coiled forms with exaggerated features such as shell thickening, the production of surplus spines or knobs, fantastic shapes and, most marked of all, considerable and illogical variation between individuals. Any change in their conditions of living pronounces a speedy death sentence on the species, but it was a pity in the interesting case of St. Helena, that the indigenous fauna could not have been left to die out in peace without the officious interference of mankind.

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VARIATION OF TERRESTRIAL GASTROPODS IN THE PHILIPPINES IN RELATION TO SHELL SHAPE AND SIZE

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(Read before the Society, 22 October 1977)

Abstract: The bicuneate distribution of shell height (h) against maximum diameter (d) discovered in various terrestrial pulmonate faunas occurs also in that of the Philippines, but with one exceptional group, the (almost entirely) endemic *Helicostylinae*, which give a scatter overlapping the two usual modes and bridging the unoccupied area between them. The unrelated *Papuininae* in northern Australasia and nearby islands show a similar but more restricted scatter. It is probable that ecological opportunities, taken independently by these two groups, are available in regions with tropical rain forest but not in other vegetational formations.

It has been shown elsewhere (Cain 1977) that fully terrestrial free-crawling stylommatophoran snails, retractable into their shells (i.e. excluding habitual burrowers, semi-slugs and slugs) do not vary at random in respect to shell height (h) and maximum diameter (d). They group bimodally, being (of whatever size) either high-spined, or more-or-less equidimensional to markedly low-spined. The faunas investigated were those of western Europe, North America, Puerto Rico, and New Caledonia, the first two in detail. These regions are taxonomically as well as geographically distinct, and it is remarkable that the same regularity is found in all. Moreover it appears again in Africa (Cain, in preparation), which is equally distinct. This paper reports the result of an investigation of the fauna of the Philippine Islands, in which, and apparently independently in New Guinea, a marked partial anomaly occurs.

MATERIALS AND METHODS

Individual adult shells were chosen as representative of their species in the collections of the Academy of Natural Sciences, Philadelphia, and at the British Museum (Natural History). (For a few species, only a single specimen was available.) They were measured as in Cain (1977). Probably too many species have been admitted for the helicostylinae snails of the Philippines, since some may be really subspecies of the same species on different islands. As the intention here is only to sample shell variation, this does not matter; no emphasis is placed on the exact density of points at any one part of the scatters.

The classification of Taylor and Sohl (1962) has been used, for consistency with previous papers, for families. The classification of the *Helicostylinae* used follows closely that in Thiele (1931) with one subsequent addition and one name-change, and is given here for convenience in consulting Fig. 2. As many forms are unknown anatomically, it can only be provisional.

FAMILY	Bradybaenidae	no. of species recognized
SUBFAMILY	Helicostylinae	
Genus <i>CALOCOCHLIA</i>		
Subgenus	<i>Calocochlia</i> Hartmann 1840	49
	<i>Pyrochilus</i> Pilsbry 1892	2
	<i>Anixa</i> Pilsbry 1894	14
	<i>Trachystyla</i> Pilsbry 1892	2
	<i>STEATODRYAS</i> Pilsbry 1932	1
<i>CHLORAEA</i>		
	<i>Chloraea</i> Albers 1850	13
	<i>Corasia</i> Albers 1850	22
	<i>Pfeifferia</i> Gray 1853	1
	<i>Chromatosphaera</i> Pilsbry 1892	4
	<i>Leytia</i> Pilsbry 1892	1
<i>HELICOSTYLA</i>		
	<i>Orustia</i> Mörch 1852	2
	<i>Pachysphaera</i> Pilsbry 1892	4
	<i>Helicostyla</i> Férussac 1891	17
	<i>Cochlodryas</i> Martens 1860	7
	<i>Opalliostyla</i> Pilsbry 1896	14
<i>COCHLOSTYLA</i>		
	<i>Helicobulinus</i> Broderip 1841	3
	<i>Rymbocochlias</i> Möllendorff 1895	2
	<i>Dryocochlias</i> Möllendorff 1898	4
	<i>Cochlostyla</i> Férussac 1819	32
	<i>Hypselostyla</i> Martens 1868	15
<i>CHRYSTALLIS</i>		
	<i>Chrysallis</i> Albers 1850	4
	<i>Dolichostyla</i> Pilsbry 1896	8
	<i>PHOENICOBIUS</i> Mörch 1852	11
	<i>PHENGUS</i> Albers 1850	2
	<i>CANISTRUM</i> Mörch 1852	4
	<i>MESANELLA</i> Clench & Turner 1952	1

The only forms I have been unable to see specimens of or obtain measurements for are *Chloraea* (*Corasia*) *irosensis* (Hidalgo) and *loheri* (Möllendorff), and *Phoenicobius anacardium* (Dohrn) and *avus* (Pfeiffer).

The classification of the papuinines is as follows.

FAMILY	Camaenidae	no. of species recognized
SUBFAMILY	Papuininae	
	<i>CRYSTALLOPSIS</i> Ancey 1887	19
	<i>FORCARTIA</i> Clench and Turner 1962	2
	<i>MEGALACRON</i> Rensch 1934	16
	<i>MELIOBBA</i> Iredale 1940	6
	<i>PAPUSTYLA</i> Pilsbry 1893	7
	<i>PAPUINA</i> Martens 1860	103
<i>RHYNCHOTROCHUS</i>		
	<i>Rhynchotrochus</i> Möllendorff 1895	16
	<i>Pompalabia</i> Iredale 1941	3
	<i>RHYTIDONCONCHA</i> Rensch 1933	2

I have seen and measured the majority of papuine species, taking a few measurements from Clench and Turner (1962, 1964, 1966) and van Benthem Jutting (1962). I have no data for *Papuina bevani* (Brazier), *chondrodes* (Strubel), *elisus* Hedley, *ferussaci* (Lesson), *pudica* (Pfeiffer), and *rhynchocheila* (Tapparone-Canefri), a total of only 6 out of 189 (?); none of these is likely to disturb the conclusions arrived at in this paper.

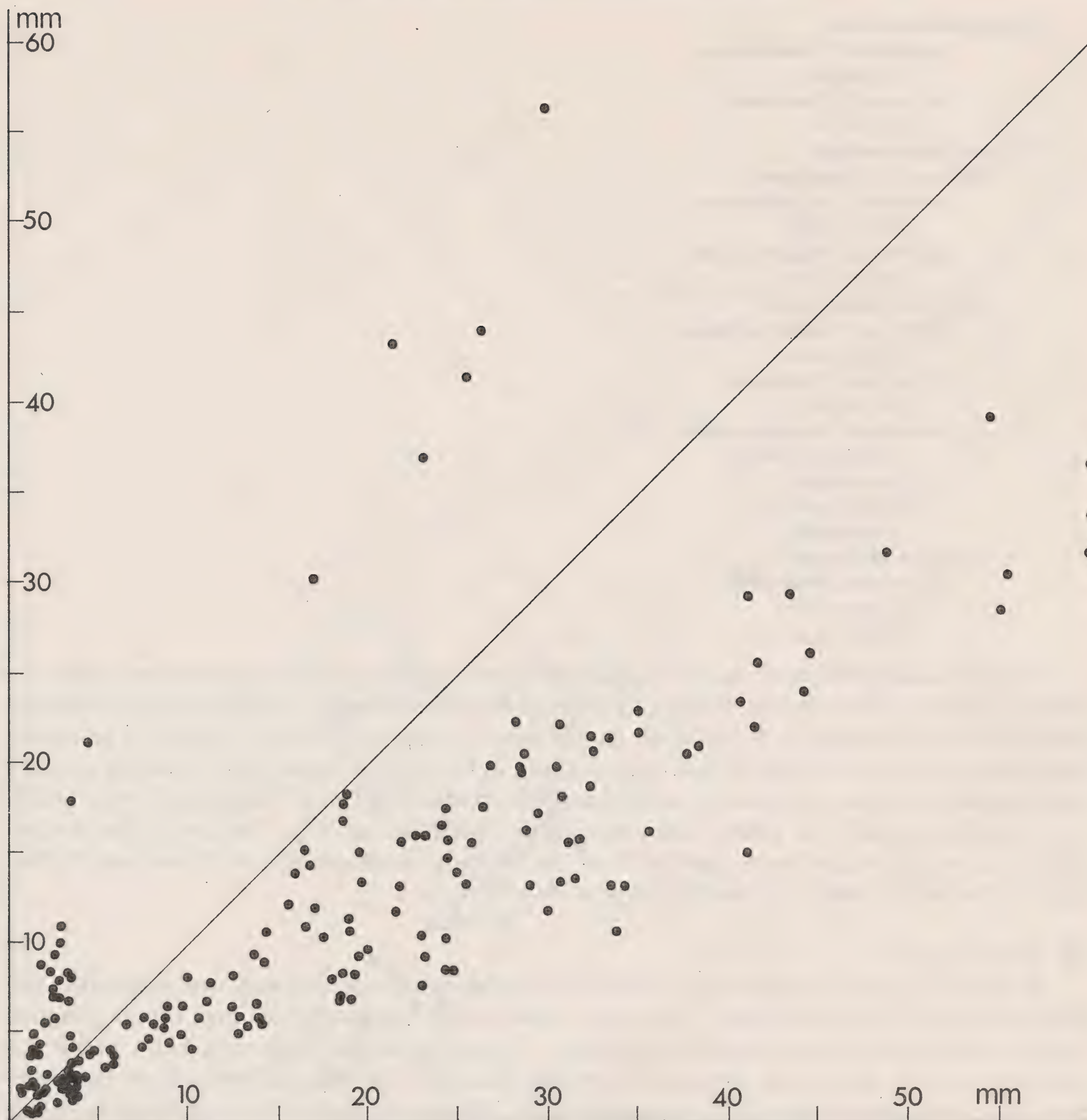


Fig. 1. Distribution of h (vertical axis) against d for land stylommatophorans of the Philippine Islands (excluding slugs and semi-slugs). The oblique line ($h = d$) serves as a reference guide.

PHILIPPINE STYLOMMATOPHORA

(i) *Stylommatophora* other than *helicostylin*es

The fauna of the Philippines has representatives of the following families, excluding slugs and semi-aquatic species, and habitual burrowers.

Suborder **Orthurethra**

Superfamily **Achatinellacea**.

Achatinellidae (Tornatellinae)

Superfamily **Pupillacea**

Vertiginidae, Pupillidae, Chondrinidae, Valloniidae

- Suborder **Mesurethra**
 - Superfamily **Clausiliacea**
 - Clausiliidae
 - Superfamily **Corillacea**
 - Corillidae
- Suborder **Sigmurethra**
 - Infraorder **Holopodopes**
 - Superfamily **Achatinacea**
 - Subulinidae
 - Superfamily **Streptaxacea**
 - Streptaxidae
 - Infraorder **Aulacopoda**
 - Superfamily **Endodontacea**
 - Endodontidae
 - Superfamily **Zonitacea**
 - Vitrinidae
 - Superfamily **Ariophantacea**
 - Trochomorphidae
 - Euconulidae
 - ? Helicarionidae
 - Ariophantidae
 - Infraorder **Holopoda**
 - Superfamily **Helicacea**
 - Camaenidae
 - Bradybaenidae

There is a sharp difference taxonomically between this fauna and that of western Europe or North America. Nevertheless, with one exception dealt with below, it falls into two modes of distribution with respect to *h* and *d*, as do the others (Cain 1977, Figs. 3 and 4). The actual distribution, except for the Helicostylinae, is given in Fig. 1. The upper mode is rather scantily represented, but shows the usual arrangement into smaller shells with *h* less than 20 mm which are very high-spined, and rather fatter ones with higher values of *h*. The lower distribution perhaps may run rather lower (further from the bisector) at values of *d* of 25 mm and higher than in the North American and European distributions.

(ii) *Helicostylinae*

No family in the Philippines is confined to that island group, and only one subfamily, the Helicostylinae (Bradybaenidae). These are large snails, some arboreal and others ground-living, with shells of diverse shapes and colours. Their distribution is given in Fig. 2 and is the first that has been found that does not fit into the bimodal distribution. It runs from the lower part of the lower scatter to within the upper scatter, filling in the normally empty space between the two. The species falling between the scatters have shells higher than wide but markedly more obese than tree-snails (for example) of the genus *Amphidromus* (Camaenidae) a few of which occur in the Philippines (Fig. 1, longest shells in the upper scatter). Ecologically, one might expect these intermediate forms to be found indiscriminately on trees and on the ground, but little seems to have been recorded of their habits.

THE PAPUININAE OF NORTHERN AUSTRALASIA

In New Guinea and neighbouring islands, there is also one endemic subfamily of stylommatophoran snails, the Papuininae, but it is classed in the Camaenidae, not the Bradybaenidae. Its scatter is shown in Fig. 3. A preliminary survey of the stylommatophorans of this region suggests the usual bimodal distribution, but, satisfactorily, the endemic subfamily again does not show it. The papuine scatter is much less widespread than the helicostyline, and differs also in one important point; the large high-spined papuines which form the genus

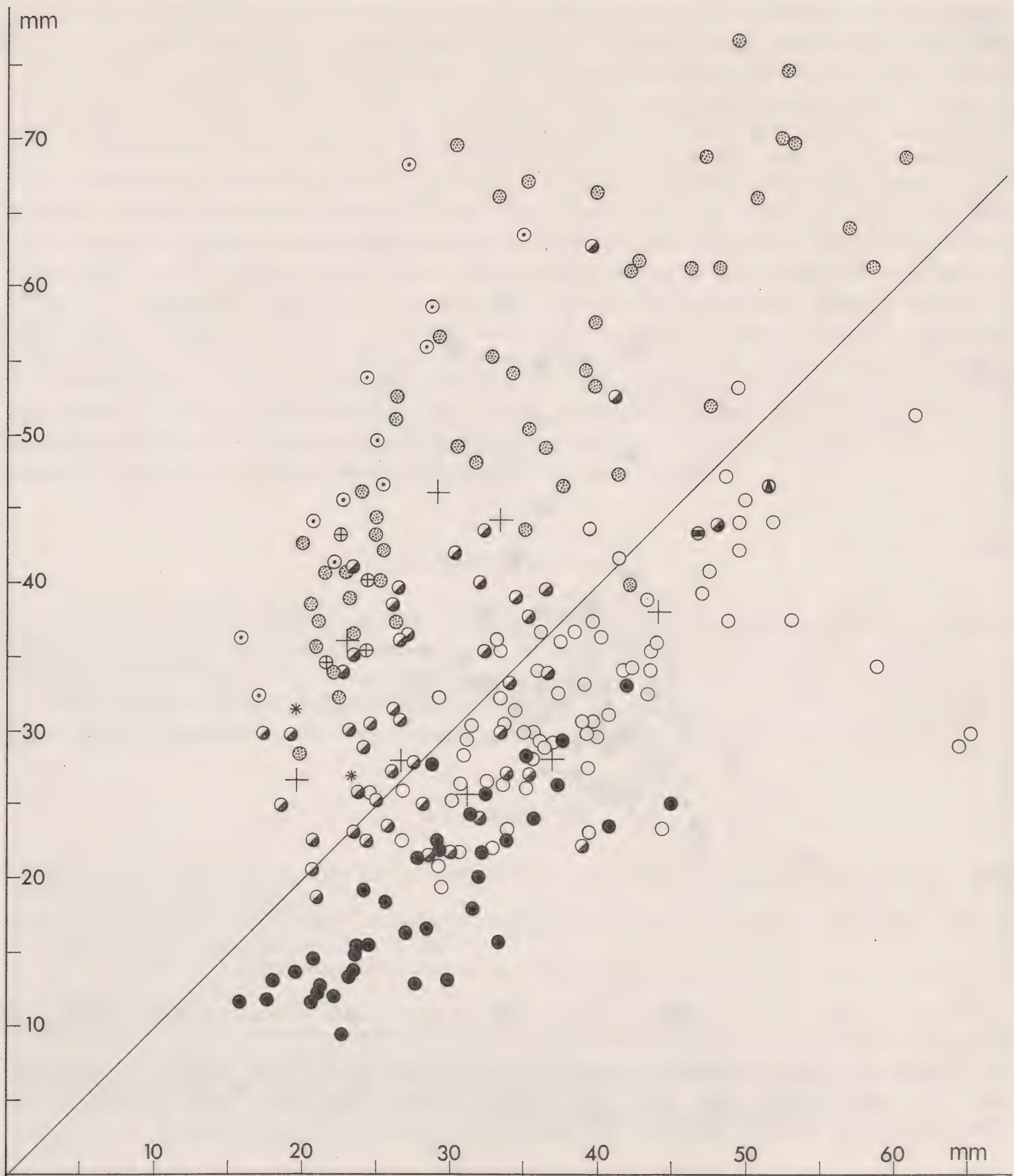


Fig. 2. Distribution of h against d for the Helicostylinae. *Calocochlia*, plain circle; *Canistrum*, circle with cross; *Chloraea*, solid black circle; *Chrysallis*, circle with central spot; *Cochlostyla*, circle with stipple; *Helicostyla*, circle half black (obliquely); *Mesanella*, circle with black triangle; *Phengus*, star; *Phoenicobius*, cross; *Steatodryas*, circle with horizontal broad bar.

Papustyla appear to be restricted to the Admiralty and Bismarck Islands. Several others in the genus *Papuina* occur in the Solomon Islands and elsewhere; only a few high-spired forms of *Papuina* are found in New Guinea itself. In the Philippines, it seems that much of the repertoire of shape and size in the helicostylines can be found on most islands, certainly on all the large ones.

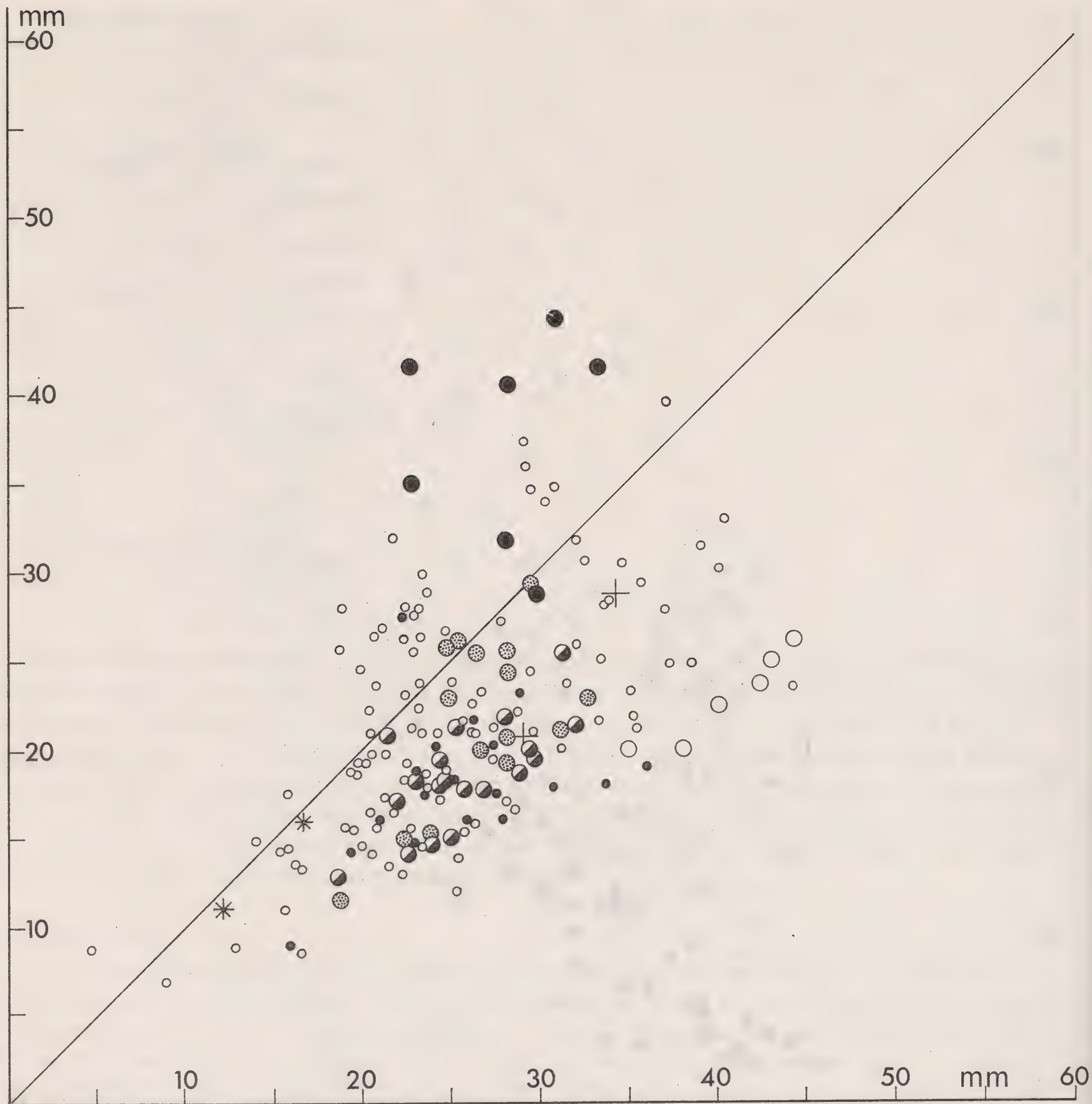


Fig. 3. Distribution of h against d for the Papuininae. *Crystalloopsis*, small solid black circle; *Forcartia*, cross; *Megalacron*, circle with stipple; *Meliobba*, large plain circle; *Papustyla*, large solid black circle; *Papuina*, small plain circle; *Rhynchotrochus*, circle half black (obliquely); *Rhytidoconcha*, star.

DISCUSSION

The discovery of a characteristic bicuneate distribution of h and d in disparate land faunas of stylommatophoran snails has given us for the first time a principle of ordination for such faunas; when regularities have been found, their significance can be investigated, and exceptions looked for. The regular occurrence of the bicuneate distribution, made up in different faunas by different taxonomic groups, indicates immediately (a) that there is a distinct and limited repertoire of shell shape and size than can be allowed to a fauna, (hence the same overall distribution-pattern for h and d); (b) that there is some interaction, probably competition,

between the groups within a fauna, (so that the overall distribution-pattern is completed by these groups) and therefore (c) that effective selection of some nature controls the values of *h* and *d* for each species within a fauna (Cain 1977). The bicuneate distribution has been proved also in various Palaearctic and African faunas, and in a mainland Oriental one (Cain, in preparation). As shown here, it holds for the majority of the Philippine stylommatophoran fauna as well. The further discovery of two independent exceptional groups, the Helicostylinae in the Philippines, and the Papuininae in northern Australasia and islands nearby, suggests that in island regions with much wet tropical forest, at least for fairly large snails, there are ecological opportunities for species of shell-shape intermediate between the two usual modes. In different regions different forms can be expected to take up these niches, as has happened with brightly coloured, high-spired shells, for example, elsewhere—Bulimulidae in tropical America, *Amphidromus* (Camaenidae) in south-east Asia and the greater islands nearby, *Placostylus* (Bulimulinae) in Melanesia, the rather enigmatic *Partula* in Polynesia, *Achatinella* and *Partulina* (Achatinellidae) in Hawaii, *Limicolaria* and *Achatina* (Achatinidae) in Africa, and so on. It is a great misfortune that so little collecting has been done with careful attention to the exact habits of different species. The interpretation of these distributions and their exceptions will almost certainly require an extended ecological analysis of these faunas.

ACKNOWLEDGEMENTS

I am deeply indebted to Dr. G. M. Davis for facilities and cordial encouragement while working on the collections of the Academy of Natural Sciences, Philadelphia, to Mr. C. L. Richardson for extensive advice and guidance on nomenclature and classification, and to Mr. J. L. Peake of the British Museum (Natural History) for facilities in studying the collections there, and information on the Papuininae he has worked on in the Solomon Islands.

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THE LIFE CYCLE OF *AEGOPINELLA NITIDULA* (DRAPARNAUD) (PULMONATA: ZONITIDAE) AT MONKS WOOD

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Abstract: From data collected over a two-year period, it is suggested that at Monks Wood *Aegopinella nitidula* has a biennial life cycle with delayed maturity and overlapping generations. This is in contrast to a previously reported annual cycle for this species. A biennial life cycle may be advantageous in unstable environmental conditions.

There has recently been considerable theoretical discussion of life-history strategies in organisms (Stearns 1976) but even in such a well-known group as the British land Mollusca, the life cycles of the large majority of species remain unknown or are at least very poorly understood. With land molluscs the situation is complicated by the apparent plasticity of their life cycles. Marked changes in fecundity, growth rate, and onset of maturation are known to occur within a species in response to often quite local environmental differences (for example Carrick 1942, Hunter and Symonds 1971, and Umiński 1975 in the Zonitacea), and this might explain the apparent conflict between many reports of molluscan life cycles in the literature. Superimposed upon this is the inherent variability between individuals within a population, which may obscure all but the most obvious patterns when only small samples are taken. This could take the extreme form of a number of genetically distinct subpopulations occurring together, each behaving differently, as has been demonstrated in some other animal groups. But evidence for this in land molluscan populations is lacking.

The zonitid snail *Aegopinella nitidula* is a common species in woodland and other generally damp habitats throughout the British Isles (Ellis 1969, Kerney 1976) and is found in Europe up to about 66°N (Ellis 1951). Rigby (1963) described *A. nitidula* as having an annual life cycle similar to the one that she described for *Oxychilus cellarius* (Müller), but unfortunately she gives no data for *A. nitidula*. In contrast, Taylor (1906-14) seems to have considered that both these species have a two-year cycle. There appear to be no other specific accounts of the life cycle of *A. nitidula*.

This paper attempts to interpret the life cycle of a population of *A. nitidula* in woodland at Monks Wood National Nature Reserve, Huntingdonshire. In addition to this field study, a number of general observations on reproductive biology are described from laboratory cultures of *A. nitidula* collected from the study area.

THE STUDY AREA

The study was made in an area of woodland in the southern part of Monks Wood, located in compartments 21 and 22 adjacent to Badger Ride (N.G.R. 52 (TL) 199798). Ash (*Fraxinus excelsior* L.) and oak (*Quercus robur* L.) of coppice origin dominate the tree layer, and the shrub

layer is composed principally of privet (*Ligustrum vulgare* L.) and coppiced hazel (*Corylus avellana* L.). Ground vegetation is generally sparse but a thick leaf litter develops over much of the area and persists during most of the year. The soil is an Oxford Clay with a pH of between 5.9 and 6.2. A more detailed account of the study area and information on climate is given in Mordan (1977) and a general account of Monks Wood with maps of the reserve may be found in Steele and Welch (1973).

MATERIALS AND METHODS

Samples of snails were taken at approximately monthly intervals between December 1968 and December 1970. For each sample twenty, 1 ft² quadrats were searched on a grid arranged as a centric systematic area-sample, the results of which approximate those from random sampling (Milne 1959). The soil surface and vegetation within each quadrat were searched, and the soil lightly grubbed to a depth of about 2 cm; all snails and eggs encountered were collected. After identification the shell breadth of each snail was measured to the nearest 0.5 mm and the animals dissected to establish sexual state. Following Bett (1960), animals were considered mature if the hermaphrodite duct contained gametes. Eggs were allowed to hatch and the newly hatched snails identified. This was necessary as it was not possible to distinguish with certainty eggs of *A. nitidula* from those of some *Oxychilus* species.

Cultures of *A. nitidula* collected from woodland adjacent to the study area were maintained in the laboratory during 1970. Snails were kept both individually and in batches at 10°C under a 12-hour light/dark regime in transparent plastic-topped boxes, and fed on vegetation and some animal food.

RESULTS

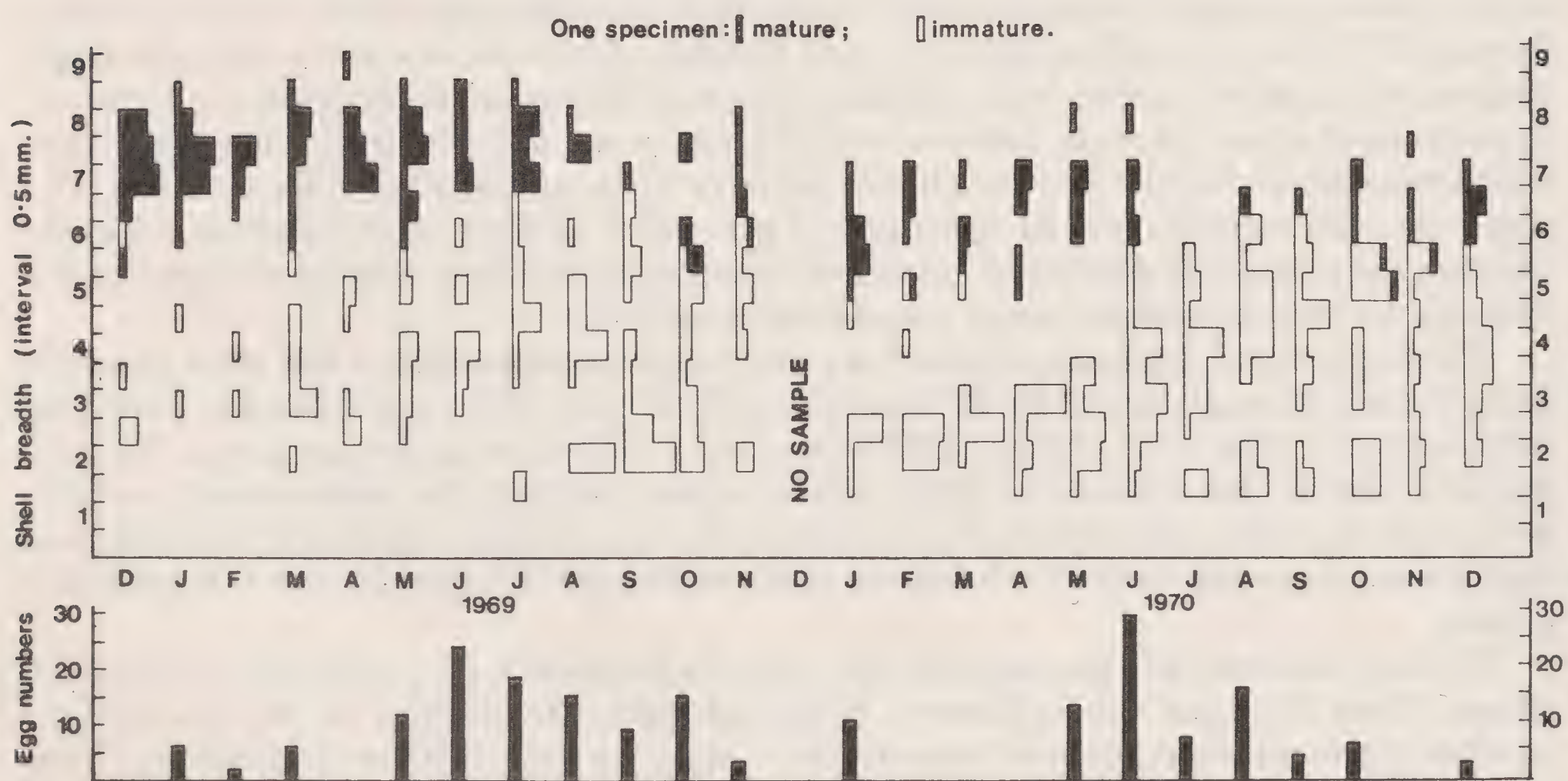


Fig. 1. Histograms showing size distribution of *Aegopinella nitidula* in monthly samples; black areas refer to mature, and open areas to immature snails. The numbers of viable eggs collected are shown below.

Field study. Size frequency histograms for *A. nitidula* and numbers of viable eggs collected during monthly sampling are shown in Fig. 1. The mean density of *A. nitidula* during the sampling period was 13.57 (s.e. ± 0.68) per m².

At the start of sampling in December 1968 two size classes were represented in the population: mature adults of between 5.5 and 8 mm, and immature individuals of between 2.5 and 3.5 mm. During the next two months the pattern remained similar with a slight upward shift in the sizes of the two groups. From May to July 1969 the size distribution of the two classes became somewhat attenuated and a small number of recently hatched snails of 2–2.5 mm appeared, presumably hatched from the few eggs recorded during the early months of the year. Not until June and July were eggs recorded in high numbers, and from July onwards that newly hatched snails (1.5–2 mm) were found in any abundance.

In August 1969 three size classes became clearly separable. There were a small number of mature adults of 7.5 mm upwards (most of the adult generation appeared to have died after laying eggs, but a few survived until November or possibly longer), a group of immature snails mostly between 4 and 5 mm in size, and juveniles of about 2 mm. In September only a single mature specimen was recorded, but by October it was clear that a large number of the snails between 5.5 and 7 mm were becoming sexually mature. Hatching appeared to continue right through until February 1970 or longer and this is in agreement with the data for egg numbers which, although showing a peak in June and July 1969, continued to be recorded until January 1970.

The picture throughout most of 1970 was similar to that in 1969. In the early months two age classes were again evident, although there were fewer adults and more juveniles than in the same months the previous year. The adult population died out somewhat earlier than in 1969 and this was reflected as a sharper peak in egg numbers around June, July and August. The highest numbers of newly hatched snails (<2 mm) appeared from July to October although, as in 1969, a number continued to hatch into the spring. From July to September very few mature snails were recorded and it was not until October onwards that many of the larger snails of 5 mm or above began to mature. In November and December the pattern became rather obscured, making interpretation difficult. Many of the larger snails had matured, but the distinction between this generation and that which hatched the previous summer (so clear in the winters of 1968/9 and 1969/70) was not obvious. This probably resulted in large part from the extended breeding period during the latter half of 1969 and early 1970, which tended to merge with that in the summer of 1970.

Laboratory study. A number of simple observations on reproductive activity were made on laboratory cultures of *A. nitidula*. Eggs were laid both singly and in small batches. In general those laid on the soil surface and amongst leaf litter usually occurred singly, whereas batches of between 9–20 eggs were found in shallow depressions about 10 mm deep in the soil. Up to 37 eggs were recorded from a single individual. In a sample of 50 eggs mean height and width were 1.6 mm (range 1.3–1.8) and 1.4 mm (range 1–1.5) respectively, thus overlapping in size with the eggs of a number of other zonitid species quoted by Frömming (1954). At 15°C the eggs hatched, on average, in 38 days and within the larger batches the range of hatching was as great as 24 days. This is considerably longer than many of the times quoted in the literature for zonitid snails but may partly reflect the culture conditions. The onset of egg laying within the cultures was remarkably well synchronized and preceded that in the field by about 4–6 weeks. A large percentage of the eggs were infertile, up to 47% in some batches, and again this may result from culture conditions; Runham and Hunter (1970) have also noted appreciable numbers of infertile eggs in some slug species.

DISCUSSION

The data for size distribution, sexual state and egg numbers of *A. nitidula* presented in Fig. 1 show a broad similarity in pattern between 1969 and 1970, suggesting that a regular cycle of growth and reproduction occurs in at least the majority of the population at Monks Wood. The following points emerge from a consideration of the data:

1. Most sexually mature adults were recorded during the first half of the year and a marked decrease in their numbers was evident after June or July.
2. There was peak in egg numbers from March to August, although limited numbers of eggs were recorded in most other months.
3. Newly hatched young were found in greatest abundance between July and October although, as with eggs, lower numbers were also recorded during other months.
4. Both during and after the peak reproductive period in late spring and summer a large proportion of the population was of intermediate size and sexually immature.

These observations, taken as a whole, are inconsistent with an annual life cycle. The relative abundances of newly hatched, intermediate, and adult snails, together with the absence of any well-defined bimodality in the size distribution of the intermediate snails, indicate a biennial cycle with a single reproductive season during the second year and overlapping generations, although the possibility of a longer cycle cannot be excluded. The relatively low numbers of snails recorded in the smaller size classes can be explained by the sampling method which would almost certainly have favoured larger individuals.

It is therefore suggested that at Monks Wood *A. nitidula* has a two-year life cycle. The snails hatch in the summer and reach sexual maturity about 18 months later during their second winter; eggs are laid in the following spring or early summer, after which most or all of the adults die. This pattern would seem to apply to most of the population but limited reproductive activity appears to occur throughout the year.

The cycle proposed above for *A. nitidula* is in broad agreement with that proposed by Hazay (1881: 115–6) for the closely related species *A. nitens* (Michaud) in Hungary. Hazay concluded that *A. nitens* reached adult size during its second year, and the relative numbers of one-year olds and adults in the population he studied suggested that few if any of the snails survived beyond two years. Gassies (1849: 108) stated that in *A. nitens* from the region of Agen in France, the eggs are laid in June, July and August, and that the species does not become adult until the end of the following year. This can be interpreted as reaching adult size or sexual maturity in either about 18 months or two years. Both accounts, however, agree in putting the cycle at longer than one year.

In discussing reproduction and development in *A. nitidula* Taylor (1906–14: 70) refers to the work of both Hazay and Gassies on *A. nitens*, considered at that time by Taylor to be a variety of *nitidula*. He also states that “growth is very slow, the shell not attaining full growth until the end of the following year” but is difficult to establish whether this is an original observation. The only recent account of the life cycle of *A. nitidula* is given by Rigby (1963). She describes the cycle of *Oxychilus cellarius* in some detail and then comments that the life cycles of other zonitids she examined, including *A. nitidula*, follow a similar pattern. Presumably observations on these other species were also made at Chorley Wood, Surrey but no data are presented. From monthly samples taken over a period of one year, Rigby described *O. cellarius* as having an annual cycle with breeding extending from January to August but with a peak in egg laying during April and May. The snails died soon after laying, only living about 14 months.

There are thus conflicting accounts of the life cycle of *A. nitidula* and it is difficult to establish whether the cycle can vary from annual to biennial or possibly longer, or whether it has simply been misinterpreted. Umiński (1975) has recently demonstrated that cycle length within a species may vary considerably over quite short distances, presumably in response to climatic changes. He showed that in the Polish Tatra Mountains the life cycles of the vitrinid snails *Vitrina pellucida* (Müller) and *Semilimax kotulae* (Westerlund) changed from annual to biennial over an altitudinal increase of only 260 m. If similar changes occur in *Aegopinella nitidula* and a biennial cycle of the type described above for Monks Wood has been developed, at least over part of its range, what are the advantages over an annual system?

Holgate (1967) has mathematically compared annual and biennial life cycles, the latter with both single and multiple reproductive seasons, and concluded that when reproductive

success varies randomly in time, a population reduces its chances of extinction by evolving from an annual to a biennial system with delayed maturity (in this case reproducing during its second year). From this it could be argued that the development of a biennial cycle is an adaptation to unstable habitats where reproductive success varies from year to year. Even though clutch size will be larger in the biennials, Holgate has shown that the mean number of offspring per individual per year is smaller in the biennial life table than in the annual when both are adjusted to yield the same intrinsic rate of increase. His arguments, however, take no account of adult size or egg size, and the relationships between these and clutch size in land snails form an intriguing problem about which there is as yet little information. With overlapping generations the chances of survival could be further enhanced by the presence, at any one time, of more than one generation, presumably with differing physiological and other susceptibilities.

The contrasting reproductive strategies associated with stable and unstable environments apparently vary according to whether mortality predominantly affects juveniles or adults (Stearns 1976). With land molluscs the principal mortality is thought to fall on juveniles (Boycott 1934: 6) and here it is predicted that late maturity, smaller reproductive effort, and longer life (all characteristics of the biennial cycle described for *A. nitidula*) are adaptations to a fluctuating environment (Stearns 1976: 26). The above arguments have assumed that cycle length is constant from year to year within a population. Short-term fluctuations in cycle length could result simply from the direct effects of climate on growth and development at an individual level.

The information available on the life cycles of other zonitid species is often equally confusing, but much of it does suggest that a generalization such as Boycott's (1934: 4) that "all are normally annuals with a life of 9–15 months" is misleading. Frömming (1954), for example, states that the life span of *Oxychilus alliarius* (Miller) is about two years and that *O. draparnaudi* (Beck) reaches maturity in 18–19 months. The weight of published evidence does favour a cycle length of greater than one year for most zonitid species for which there are data, but until the results of more-detailed investigations over a range of climatic and habitat types are available it would seem unwise to be other than cautious.

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BRITISH FORMS OF *LIMAPONTIA DEPRESSA* ALDER AND HANCOCK, 1862 (OPISTHOBRANCHIA: ASCOGLOSSA)

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(Read before the Society, 19 November 1977)

Abstract: The literature is reviewed and observations are made on some recent records. *Limapontia depressa* is found not only on salt marshes but on the mud of estuaries, coves and inlets of the sea. Its habit of burrowing in wet mud suggests it was once an infaunal species. It feeds on *Vaucheria* and associated green algae, and on one occasion was observed feeding on *Cladophora*. The main anatomical differences between *L. depressa* and *L. capitata* are described. *L. depressa* may be regarded as a polytypic species with three subspecies: *L. depressa depressa* Alder and Hancock (black); *L. d. olivaria* nov. (dark olive to brown); and *L. d. pellucida* Kevan (chrome yellow and green).

REVIEW OF LITERATURE

Hancock's description of *Limapontia depressa* published in 1862 is a model of accurate observation and concise statement and is quoted in full.

Description of a new species of naked Mollusca by Albany Hancock, F.L.S.

Family Limapontiadae

Limapontia depressa n. sp. PL. XVII.

Body, oblong-ovate, depressed, swelling behind the centre and terminating in a blunt point posteriorly, but varying much according to the degree of expansion or contraction; black with minute yellowish-white spots or freckles, not always present, and very inconspicuous. *Head* rounded in front, and slightly angulated at the sides; the lateral crests less elevated than in *L. nigra*, with the eyes situated near the centre of a white oblong area at the side of each. *Anus* placed in a depression at the posterior extremity of the body. *Foot* yellowish-white, linear, and squared in front.

Length upwards of a quarter of an inch.

A few individuals of the species were obtained, last October, in brackish-water pools at the mouth of Hylton Dene, near Sunderland, associated with *Alderia modesta* on a *Conferva* (*Vaucheria submarina*?).

The species referred to by Hancock is *Limapontia nigra*, Johnston, 1836. In 1774 Müller had described the same species and named it *Fasciola capitata* (he thought it was a flatworm). In accordance with the principle of priority (International Code 1964) it is now known as *Limapontia capitata* (Müller). Hancock's water-colours of *L. depressa*, preserved in the Hancock Museum, Newcastle upon Tyne, depict the body colour as brown, and this suggests he had also seen individuals on the surface of the saltings, for some of these are brown in colour. In the North

Country, a dene is a small wooded valley through which a burn, or stream, flows. About twenty years ago most of the lower part of Hylton Dene was filled in and levelled, and now a new road runs across it. Fortunately, the small saltings at the mouth of the burn still remains; so that the type locality of *L. depressa* has not been lost, though it is in need of preservation.

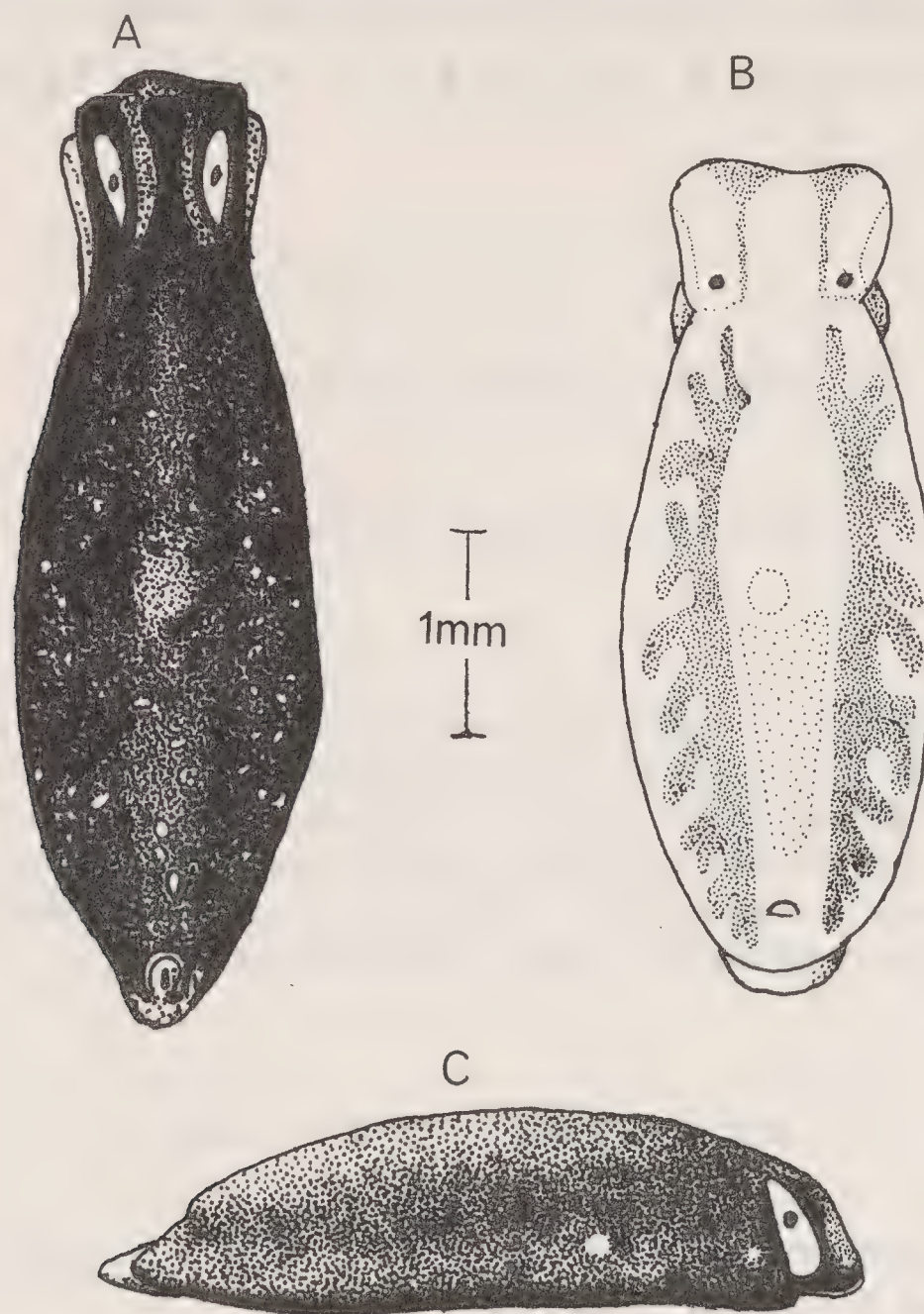


Fig. 1. Subspecies of *Limapontia depressa*. (A), *L. depressa depressa* (black); (B), *L. depressa pellucida* (yellow and green); (C), *L. depressa olivaria* (dark olive to brown). A, after Hancock (1862); B and C, after Quick (1950). The animals can vary in shape; when touched they often contract into button-shaped blobs.

Alder (1869) summarized Hancock's description in Jeffrey's *British Conchology*, Vol. 5; and Eliot (1910) quoted Alder's summary in his supplement to Alder and Hancock's *A monograph of the British nudibranchiate Mollusca*. Neither Alder nor Eliot added anything that was new, although Eliot remarked there was apparently no record of the species since the days of Alder and Hancock. There was, in fact, one record: Petch (1903) found *L. depressa* at Easington, Humberside.

In 1934 D. K. Kevan, a member of the Conchological Society, published an important paper on *L. depressa*. He studied a population present on a saltings near Tynninghame, Lothian, Scotland. In mid-April he found *L. depressa* to be abundant not only in pools, but in places where the surface of the mud, at some distance from the pools, was sufficiently damp. Here, then, was a semi-terrestrial ascoglossan. He observed that the colour of the species was not only black, but also dark olive, and noted a pellucid, or 'pale' form, in which the body colour was chrome-yellow with the green of the gut showing through. The animals were present in numbers during the months of March to June, after which they disappeared, save for a few stragglers. Kevan sensibly supposed that *L. depressa* spent about eight months as veligers in the estuary or nearby sea; then changed to adults on the salt marsh, where they lived for a few months, laid their eggs, and died. He assumed that the black forms in the estuary were *L. capitata* and thought that the pellucid form, which he called a variety, might be a new species, but realised that only an examination of its internal anatomy could settle the question.

About the same time Nicol (1935) was studying the ecology of a salt marsh near Aberlady, Firth of Forth, Scotland. Nicol apparently mistook the black forms of *L. depressa* for *L. capitata* for she stated that although *L. capitata* was occasionally reported from rock pools near high water mark, its most characteristic habitat was the pools of salt marshes. Kevan (1939) published a zonal study of Tynninghame saltings and the adjacent estuary. He observed that *L. capitata* was common on the estuarine mud and that dark olive and pellucid forms of *L. depressa* were common on the salt marsh. He found a few black forms in the salt marsh pools.

In 1941 D. K. McE. Kevan (son of D. K. Kevan) published the results of some experimental work. He collected *L. depressa* from Tynninghame marsh in December and kept them in tanks in which different habitats were simulated: completely submerged mud; mud and algae only partly submerged; and mud with vertical sides high out of the water. The water was taken from the sea and the animals were supplied with *Vaucheria* from the salt marsh. All animals lived for six weeks and those totally submerged lived on to the end of July. This demonstrated that the species thrives when submerged and can exist in semi-terrestrial conditions. D. K. Kevan's son was convinced that the black forms present in salt marsh pools were not *L. capitata* and said so in capital letters! He named the yellowish-green form *L. depressa pellucida*, thus giving it subspecific status.

The interest of field naturalists was now aroused. In 1934 and 1944 McMillan had already found the dark olive and pellucid forms on the firm, damp mud of a salt marsh near Bromborough, Cheshire. The two forms were present in approximately equal numbers and were feeding on *Vaucheria* spp. (personal communication). In 1949 she found the black form in brackish-water pools on the same marsh. Quick (1950) recorded the dark olive form near the Loughor estuary, Glamorgan, where Spence Bate, J. Gwyn Jeffreys (author of the well-known British Conchology) and Moggridge had found it in 1849—twelve years before Hancock's discovery. However, Spence Bate in his report identified the animals as *L. nigra*; he published three figures, but gave no description. Hancock (1862) was convinced that the Hylton Dene individuals belonged to a new species, which he named *L. depressa* because of the flattened or depressed shape of the body.

Quick's admirable paper of 1950 summarized what was then known about *L. depressa*; he mentioned all past records and papers and this helped me greatly when writing the present paper. Quick was a good artist and his drawings of *L. depressa* and the subspecies *pellucida* are clear and natural. His descriptions of the external features are likewise very good, and his remarks about the movement of *L. depressa*, its egg mass, and development of the veliger, evince his keen powers of observation.

RECENT RECORDS AND OBSERVATIONS

In 1976 and 1977 members of the Conchological Society recorded *L. depressa* present on many salt marshes and in some estuaries and loughs, including: Gower Peninsula, Glamorgan, and Dolgellau, Gwynedd (J. Chatfield); Pagham Harbour, Sussex, Beaulieu River, Hampshire, and Carna, Ireland (T. Gascoigne); the Bristol Avon (C. T. Hayton); Mersea Island, Essex (Joan L. Jones); River Thames near Southend on Sea (John L. Jones); Strangford and Larne Loughs, Northern Ireland (E. Platts); Kirkwall, Orkney, Scotland (I. F. Smith); Aberlady and Tynninghame, Lothian, and Seilebost, South Harris, Outer Hebrides (S. M. Smith). In 1940 *L. depressa* was thought to be rare, but these and other records show that it is a common species of British salt marshes.

On the saltings at the landward end of Strangford Lough, Ireland, a number of *L. depressa* were found on the firm mud, and Elizabeth Platts noticed a vast population of the black form living in the water at the edge of low tide. The situation at Lough Larne was similar. Most of the *L. depressa* were found on the mud in the shallow water along the margin of the lough and a

lesser number were present on the fringing salt marsh. And again, John L. Jones noted a large population spread over submerged mud-flats near Southend on Sea. Black forms from these three locations were checked by fine dissection to make sure they were *L. depressa*. Hitherto *L. depressa* has been regarded as a salt marsh species (Thompson, 1976), but its range is more extensive than this. It is essentially an estuarine species and its range extends into the gullies and pools and on to the damp mud of salt marshes.

Shelagh M. Smith visited the salt marsh at Aberlady where she found *L. depressa* common, but *L. capitata* absent. At one spot, just about two hundred yards from the salt marsh, a low limestone reef ran out into the Firth of Forth; and in small pools on the reef *L. capitata* was common. She visited Tynninghame saltings and recorded *L. depressa*, but not *L. capitata*. About half a mile away *L. capitata* was found in rock pools. I accompanied S. M. Smith on her visits and obtained specimens which were examined by fine dissection and this confirmed her identifications. We did not find *L. capitata* in the pools of the salt marsh studied by Nicol, and none of our members has reported *L. capitata* as present on salt marshes.

L. depressa is known to feed on *Vaucheria* and associated algae that form green patches and cushions on salt marshes. Occasionally it feeds on other seaweeds. For example, John L. Jones found some *Cladophora* growing in pools formed by gravel and boulders that had sunk in the mud of the Thames. A number of limapontiids were found feeding on the *Cladophora*. At first, it was thought these were all *L. capitata*, but subsequent dissections proved that several were black forms of *L. depressa*. It is likely that *L. depressa* will be found feeding on *Chaetomorpha*, but so far, we have no record of this.

Joan L. Jones sent me an interesting letter which she kindly permits me to quote: 'Last Spring, near Colne Point, Essex, we reached a large gully with very steep sides just as the tide was receding—the banks were sparsely covered with *Salicornia*, *Vaucheria* and other algae. When we arrived the tide was just below the top of the banks which were thickly carpeted with *L. depressa* and *A. modesta*. Ten minutes later we could not find any of these animals—they had, presumably, all disappeared into the mud'. This habit of burrowing in mud (also less strikingly noted on other occasions) may be correlated with the flattened body and low crests of *L. depressa*. Indeed, *L. depressa* may have been an infaunal species that, in geologically recent times, has followed its algal food on to the surface of salt marshes.

INTERNAL ANATOMICAL DIFFERENCES BETWEEN *L. DEPRESSA* AND *L. CAPITATA*.

Most guide books contain good descriptions of *L. depressa* and *L. capitata* that are usually adequate enough to distinguish between the two species. However, estuarine black forms of *L. depressa* are still sometimes mistaken for *L. capitata*, and poorly-preserved, contracted specimens of *L. depressa* may cause trouble. In order to be certain of the species it may be advisable to have recourse to fine dissection; and to assist identification by this means the main differences between the internal anatomy of *L. depressa* and *L. capitata* are now described.

L. depressa and *L. capitata* have distinctly different penial styles (Fig. 2, B and E). Had this been known in 1930 the two species would not have been confused. The style of *L. capitata* is a slightly curved cuticular tube of diameter 10 μ m and length 50 μ m; its opening has a lip-like thickening on one side (Fig. 2E, l) and there are no spines on the shaft. It was described and figured by Alder and Hancock in 1848. The style of *L. depressa* has a diameter of about 30 μ m; the opening is long (80 μ m) with the rim turned slightly inwards so that it appears irregular when a coverglass is placed over it. The shaft is curved somewhat like a teapot spout and on the inner curve of the shaft are a few recurved spines (sp) of length about 4 μ m. It was described and figured by Gascoigne (1956).

In *L. depressa* the rectum (Fig. 2A, r) is long and the anus (a) lies dorsally on the median line

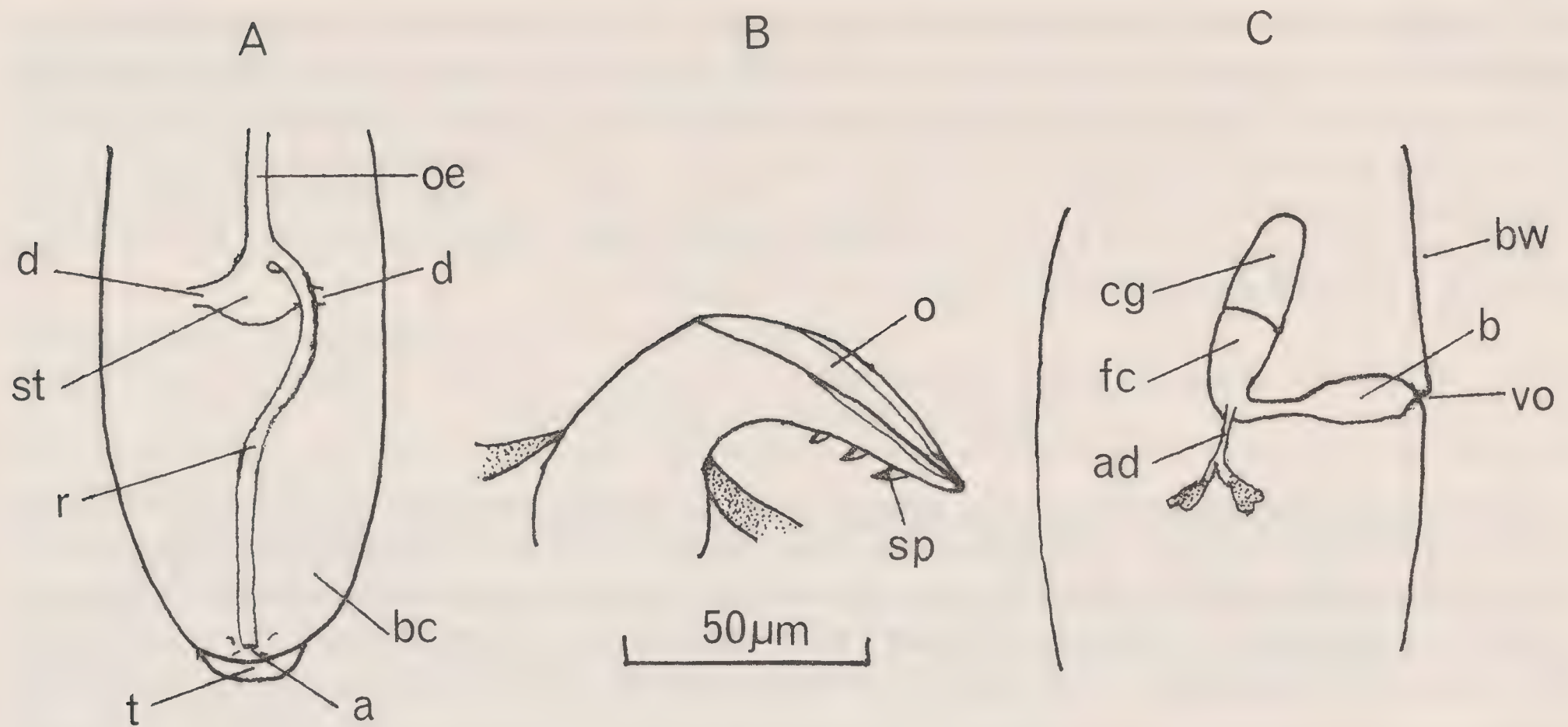
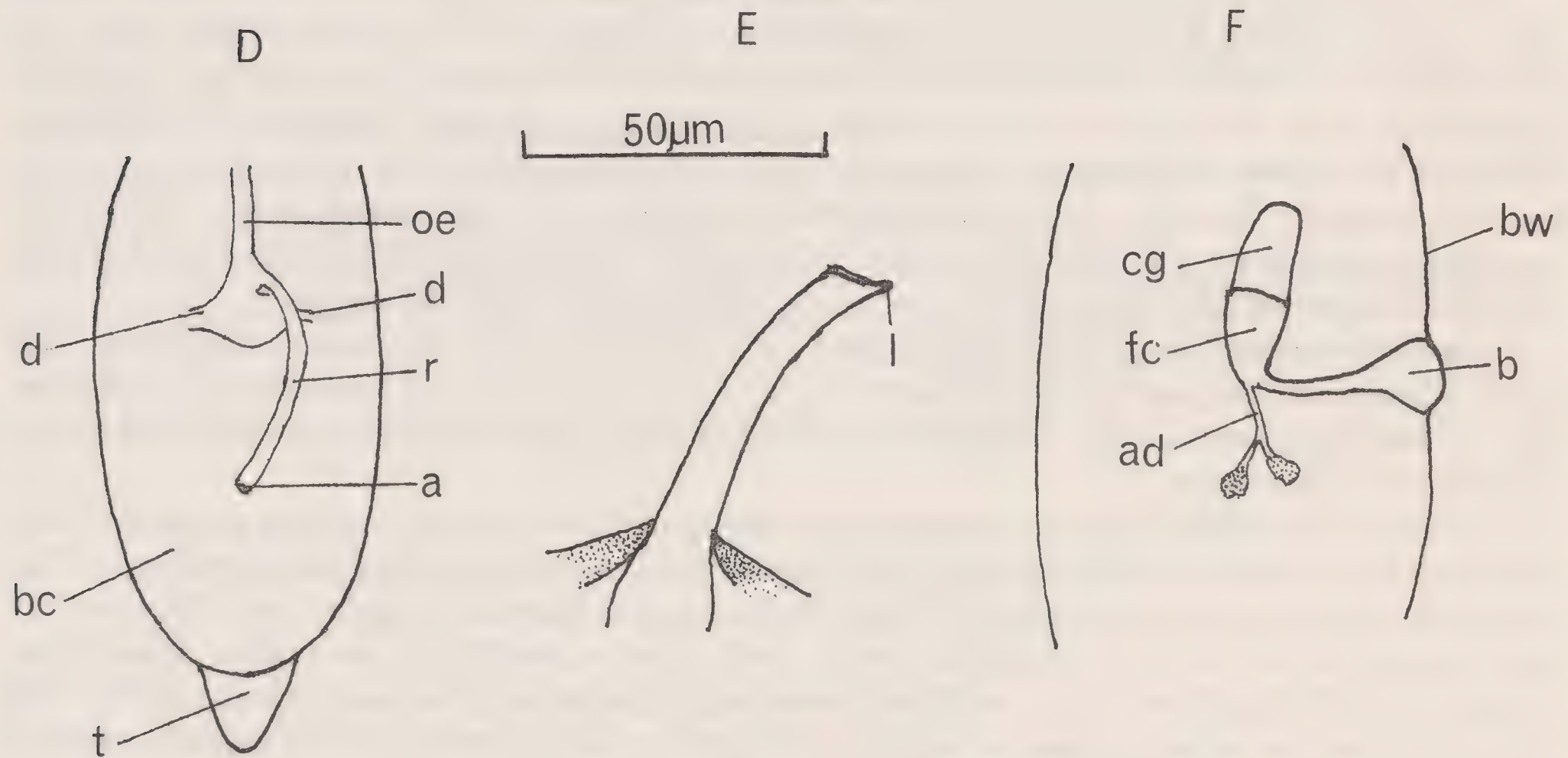
L. depressa*L. capitata*

Fig. 2. Internal differences between *L. depressa* and *L. capitata*. A and D, anal openings; B and E, penial styles; C and F, bursae. B and E were drawn from preparations in Berlese's fluid; the remaining figures are diagrammatic.

a, anus; ad, main albumen duct; b, bursa copulatrix; bc, body cavity; bw, body wall; cg, capsule gland; d, main duct from stomach; fc, fertilization chamber; l, lip; o, opening of style; oe, oesophagus; r, rectum; sp, spine; st, stomach; t, tail; vo, vaginal opening.

Dissection notes. To trace the rectum relax the animal and preserve it in Carriker's fluid for two days. Pin out dorsally and open along the mid-dorsal line; stain for about 20 minutes in acetocarmine. Trace the oesophagus from the buccal mass to the stomach and follow the course of the rectum to the anus. For the bursa and duct find the bursa (it lies about half way along the right side) and follow it to the fertilization chamber. To make a preparation of the penial style it is advisable to remove the right eye together with the penis and place on a slide in two or three drops of Berlese's fluid. With the aid of a dissection microscope at a magnification of $\times 50$ and using fine needles, remove the eye, clear the penis from tissues, and display the penial style. Examine it first *without* a coverglass by means of a microscope with a low power objective (N.A. 0.25); then put a coverglass on and use an objective of N.A. 0.65, total magnification $\times 600$.

in a small depression on the surface at the end of the body. The rectum of *L. capitata* (Fig. 2D, r) is shorter and the anus lies near the median line about one-third the way from the end of the body.

L. depressa is triaulic and the bursa copulatrix (Fig. 2C, b) opens to the exterior in a vaginal opening (vo). *L. capitata* is pseudo-diaulic; there is no vaginal opening, and the bursa is attached to the inner side of the body wall. During copulation the style is thrust through the body wall of the partner and sperm are injected into the bursa. The vaginal opening of *L. depressa* lies in a depression usually surrounded by a pale area, whereas in *L. capitata* the bursa often bulges outwards with a pale streak behind it. With a $\times 8$ lens this difference may be seen in living animals, provided the light is good and one has patience.

SUBSPECIES OF *L. DEPRESSA*

There are three colour forms of *L. depressa*: animals living submerged are black; those living on the surface of the marsh are mainly dark olive to brown; and there is the yellowish-green form recognized by Kevan. The three forms have been examined many times for specific differences in internal anatomy, but none was found; their alimentary, reproductive and nervous systems are similar. In particular they possess the same penial style and vaginal opening, so that the forms are not reproductively isolated from one another by differences in genitalia. They cannot, therefore, be regarded as separate species on anatomical grounds.

The colour is due to a melanin which is deposited in granules at the base of epithelial cells. In the estuarine forms the granules are numerous and black, so that, with few exceptions, the animals are of a uniform black colour, save for pale stripes on the head and crests and pale areas around the eyes. The dark olive forms produce a brown melanin and its disposition is variable; thus one sometimes sees animals with a pale patch over the heart, or flecks along the back and sides of the body. There are few melanic granules in the epithelial cells of the chrome-yellow and green form which is an albino with respect to melanin. The chrome-yellow appears to be a fat-soluble compound and the green is due to the chloroplasts stored in the gut.

Possibly the kind of melanin depends on the species of algae on which the animal feeds. The albino form may not take in with its food the phenolic compounds necessary for the production of a melanin pigment; or the albinism could be caused by a genetic mutation which blocks the production of melanin.

According to Mayr (1969) a subspecies is a group of populations occupying a separate part of the species range and differing from other populations of the species in a taxonomic way. The dark olive to brown form satisfies all these conditions; it is found in populations, it lives on the salt marsh rather than in brackish water, and is recognizable by its colour from other populations. Using trinomials, the black nominate species is *L. depressa depressa* Alder and Hancock; and the olive to brown subspecies, I suggest, could appropriately be called *L. depressa olivaria* nov. The pellucid form, however, does not occur in a separate part of the species range, for it lives alongside *L. d. olivaria*. Nevertheless, a case can be made out for regarding it as a subspecies rather than a variety. It exists in populations on many salt marshes and is so distinct in colour that it is frequently mistaken for a new species. Moreover, Hinde and Smith (1974) state that the pellucid form shows signs of chloroplast symbiosis, whereas the darker forms do not. It probably uses as food the products of photosynthesis, for in an experiment it survived a period of 14 days starvation with negligible loss of weight. This would help it to survive on salt marshes during temporary unfavourable conditions. It may be a species in evolution and could be called *L. depressa pellucida* Kevan.

The three named subspecies are useful taxonomic additions for they help us to realise the range and evolution of the species. It can flourish in estuaries, provided it can find sufficient food; it has obtained a foothold on land, albeit in damp marshy conditions; and one subspecies obtains some food by chloroplast symbiosis.

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OXYCHILUS HELVETICUS (BLUM) (PULMONATA: ZONITIDAE) NEW TO IRELAND

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(Read before the Society, 22 October 1977)

Abstract: *Oxychilus (Ortizius) helveticus* (Blum) is reported living in Co. Limerick, in SW Ireland. Though this species is widespread in England and Wales, all previous Irish records from open habitats are thought to be erroneous. The disturbed nature of the newly discovered sites suggests that it may be a relatively recent introduction.

The zonitid snail *Oxychilus helveticus* is locally common in England and Wales (Kerney 1976, map 116). Abroad it occurs in Switzerland (the type locality is near Solothurn, in the Jura mountains), the western Pyrenees, northern France, and Belgium. Some old records exist for Ireland, summarized by Taylor (1907, 3: 55 and plate V). Shells from Bantry, Cork West (Irish Grid square V 94) and Whitegate, Cork East (W 86) were indeed identified by Blum himself as belonging to his species (Phillips 1894). Nevertheless, in the mature opinion of Phillips (1910), Stelfox (1910) and Kennard (1910) all these records are almost certainly erroneous, being based on dark, high-spined forms of *O. cellarius* such as are unusually common in this part of the British Isles and which superficially may resemble *O. helveticus* fairly closely. Dr. P. B. Mordan has kindly discovered for me that the original shells from Bantry seen by Blum are now preserved in the Department of Zoology, British Museum (R. F. Scharff leg. 8. ii. 1894; J. W. Taylor coll.; reg. no. 197786); Dr. Mordan and I agree that they are only high-spined examples of *O. cellarius*, and not *O. helveticus*. *O. helveticus* has however once been found in Ireland as a hot-house alien at Hillsborough Castle, Co. Down (recorded as *rogersi* Woodward; Stelfox 1911). No further Irish records have since come to light.

In September 1977, in the course of systematic 10-kilometre square grid mapping for Mollusca in southern Ireland, a Conchological Society party (Mrs. M. Fogan, R. C. Preece, Mrs. E. B. Rands and the writer) discovered *O. helveticus* living in Co. Limerick. Three sites were detected, all lying within grid square R(11)32, a few miles south east of Newcastle West. The shells were quite similar to those from localities in southern England, and the living animal showed the characteristic jet-black mantle edge, a feature not shared by any other British zonitid. Alcohol material has been deposited in the Ulster Museum, Belfast, and in the British Museum (Natural History), London.

The sites are as follows:

(1) Roadsides 3 km NW of Broadford (R 317238). *O. helveticus* was common in rather damp grass and below stone walls. The associated species were *Cochlicopa lubrica*, *Lauria cylindracea*, *Discus rotundatus*, *Vitrea contracta*, *Oxychilus cellarius*, *Deroceras reticulatum*, *D. caruanae*, *Clausilia bidentata*, *Trichia striolata*, *Cepaea nemoralis* and *Helix aspersa*.

(2) Road junction near Feohanagh, 4 km NNE of Broadford (R 348253). *O. helveticus* was here very abundant under fallen branches and other ground litter in a damp spinney by an abandoned stable yard. One piece of wood carried 30 or 40 living examples. The associated species were *Cochlicopa lubrica*, *Leiostyla anglica*, *Discus rotundatus*, *Arion subfuscus*, *A. hortensis*, *Oxychilus cellarius*, *Milax budapestensis*, *Limax grossui*, *Deroceras reticulatum*, *D. caruanae*, *Trichia striolata* and *Cepaea nemoralis*.

(3) Broken Bridge, 3 km SSW of Kilmeedy (R 359270). *O. helveticus* was found abundantly north of the river bridge, mainly among rubbish in a concrete culvert, associated with *Arion hortensis*, *Oxychilus cellarius*, *Milax sowerbyi*, *M. budapestensis*, *Limax grossui*, *Deroceras reticulatum*, *D. caruanae* and *Trichia striolata*.

Oxychilus helveticus was by far the most common zonitid at all three sites. This gregarious behaviour is also typical of the species in England. The sites share certain features. Though within a limestone area, they are on heavy soils and rather dank. All show disturbance, human rubbish being particularly evident at Feohanagh and Broken Bridge. Many of the associated molluscs are characteristic of synanthropic faunas in Ireland, especially *Milax sowerbyi*, *M. budapestensis*, *Limax grossui* and *Deroceras caruanae*.

So it may be that *O. helveticus* is a fairly recent introduction at these places. No doubt it will be found to occur in many comparable synanthropic habitats in this immediate area, in the low-lying country around the headwaters of the River Deel in grid squares R 32 and 33. Whether it lives also in more natural habitats—so far as these exist at all in this virtually deforested area—can only be established by a more thorough survey; at present there is nothing to suggest that it is a native Irish species. Though widespread in Britain, both in relatively wild and in humanly disturbed habitats, it is worth pointing out that no certain early Postglacial fossil records exist, and the species may therefore well have been introduced and spread within these islands by man.

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ANATOMICAL OBSERVATIONS ON *POMATIAS SULCATUS* (DRAPARNAUD, 1805) (PROSOBRANCHIA: POMATIIDAE)

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(Read before the Society, 22 October 1977)

Abstract: The genital system and radula of *Pomatias sulcatus* are described and contrasted with those of *P. elegans*. Differences occur in both the male and female genital systems and in the radula where the central and lateral teeth have more denticles in *P. sulcatus* than in *P. elegans*.

Resumen: Según nueastros datos, *Pomatias sulcatus* solamente vive en regiones costeras del mar Mediterráneo y del sur de Portugal, y hasta ahora solo ha sido encontrada en España, fósil, en las provincias de Gerona y Almería. En este trabajo damos a conocer el hallazgo de una población actual de *Pomatias sulcatus* en la provincia de Granada; describimos su concha, aparato reproductor y rádula y, comparándolos con los de *Pomatias elegans*, indicamos las principales diferencias observadas entre ambas especies con respecto a ellos.

There are many works about the morphology, anatomy, physiology, etc., of *Pomatias elegans* (Müller 1774) (Alonso and Ibáñez 1977) because it is one of the more common prosobranchs in Western Europe. However, few data are known concerning other species of Pomatiidae such as *Pomatias sulcatus* (Draparnaud 1805). The anatomy of this species was unknown in 1965 (Forcart 1965), and at the present time Dr. Forcart (personal communication) and we ourselves are unaware of the existence of any descriptions of it.

According to our data (Forcart 1965; Germain 1931; Llabador 1938; Nobre 1941; Picard 1949 and Sacchi 1954), *Pomatias sulcatus* only lives in the coastal regions of the Mediterranean Sea and of southern Portugal.

In Spain, fossils of this species have only been found in Palau Sacosta (Gerona) (Bofill *et al.* 1921), La Pita Calataray (Almería) (Gasull 1972) and San Juan de Terreros (Almería) (A. Cobos, personal communication). In Hidalgo's work there is also a record of 'Sur de España', without a precise locality and without any indications whether the specimens were alive or whether they were fossils.

In August 1976 and March and April 1977, we found 130 specimens of *Pomatias sulcatus* (20 alive) in the 'Tajo de Escalate' (Motril, Granada, Spain), whose U.T.M. co-ordinates are: 30SVF5271. This place is 7.5 kms from the coast, on a mountainous slope (100 m altitude) at the base of a rocky wall and with typical Mediterranean vegetation.

All the specimens that have been found were partially buried, and only under *Chamaerops humilis* (L.), which is apparently its food.

Among the malacological fauna that accompanies *Pomatias sulcatus* are the following species: *Iberus alonensis* (Férussac 1817); *Iberus loxanus* Rossmässler 1854; *Ferussacia folliculus* (Gronovius 1781); *Caracollina lenticula* (Férussac 1821) and *Sphincterochila* (*Cariosula*) *cariosula* (Michaud 1833).

The features of our population are the following: the body is whitish, with grey stains on the

head and sides of the foot; the foot is cleft by a deep groove into a right and a left half, which are moved alternately in walking as in *Pomatias elegans*.

The shell (Fig. 1) is solid, ovate, conical and somewhat swollen. There are $4\frac{1}{2}$ –5 whorls, separated by a deep suture. The body-whorl is very big; the height of the body-whorl is almost half the shell's height. The apex is smooth and yellow in colour. The aperture is subangular above; the peristome is continuous and very prominent; it is also rather thick and somewhat reflected. The shell has transverse axial ridges, which are wavy, close and very narrow; there are also spiral ridges much less prominent and more widely spaced than the transverse ridges.

The colour is yellowish or orange-coloured, paler within the aperture, with transverse, irregular orange bands, very highly coloured. The thick operculum is located on the metapodium in a central position, and is deeply sunk within the aperture; the external surface is almost smooth and the internal surface shows deep radial striae and marked spiral striae.

In our population, we have found a pronounced sexual dimorphism, the females (21.6–23.5 mm height and 14.4–16 mm wide) being considerably larger than the males (17.6–19.9 mm height and 12.5–14 mm wide).

The genital system is basically similar for both sexes. It extends along the columellar side of the visceral mass. The genital duct opens into the mantle cavity in the female, while in the male it continues through the penis which lies behind the right cephalic tentacle. For the description of the genital system, we have employed the nomenclature used by Creek (1951).

Male genital system (Fig. 2): the testis is located inside the digestive gland, in the upper coils of the visceral mass. It is formed by numerous whitish tubules that join and form ducts that lead into the thin vas deferens. This vas deferens widens into a very long vesicula seminalis with a large number of little folds; towards the anterior end of the vesicula seminalis, the renal vas deferens is located which connects the spindle-shaped prostate. The posterior half of the prostate is embedded in the visceral mass and its anterior half is located in the mantle cavity. The pallial vas deferens departs from the prostate and ends in the thick and muscular penis.

Female genital system (Fig. 3): the ovary is formed by a single and intense yellow tubule, located inside the digestive gland; the ovary continues along a narrow and long oviduct that after widening becomes the receptaculum seminis, which is long and has folds. The terminal portion of the duct is the renal oviduct, that opens into the bursa copulatrix, which is located almost completely in the visceral mass. The opening of the bursa copulatrix is continuous without interruption with a wide and elongated opening, which extends along the right side of the mantle skirt. The pallial oviduct lodges the albumen gland and the capsule gland, both very large.

The radula has numerous rows with 7 teeth each (Fig. 4). The central tooth (Figs. 5–6) is triangular with the apex curved, and has 5–7 denticles; the central denticle is thick with the end rounded; the first lateral denticles, right and left, are divergent, sharp-pointed and thinner, and the last two lateral denticles of each side are very small. The first lateral tooth (Figs. 5 and 7) has 5 denticles with one bigger than the others and rounded, while the other denticles are shorter and sharp-pointed. The second lateral tooth (Figs. 7–8) is rectangular and has 4–5 denticles, all sharp-pointed which do not stand out over the others. The marginal tooth (Fig. 9) has the denticles separated in 2 groups, the first group has 6 denticles and the second group has 10–12 denticles; all the denticles have clear separation between them.

Plate 5 (opposite)

Fig. 1. *Pomatias sulcatus*: male (left) and female (right). $\times 2.5$.

Fig. 2. male genital system 1: testis; 2: vas deferens; 3: vesicula seminalis; 4: renal vas deferens; 5: prostate; 6: pallial vas deferens; 7: penis.

Fig. 3. female genital system 1: ovary; 2: oviduct; 3: receptaculum seminis; 4: renal oviduct; 5: bursa copulatrix; 6: albumen gland; 7: capsule gland; 8: opening of pallial oviduct.

POMATIAS SULCATUS (DRAPARNAUD)

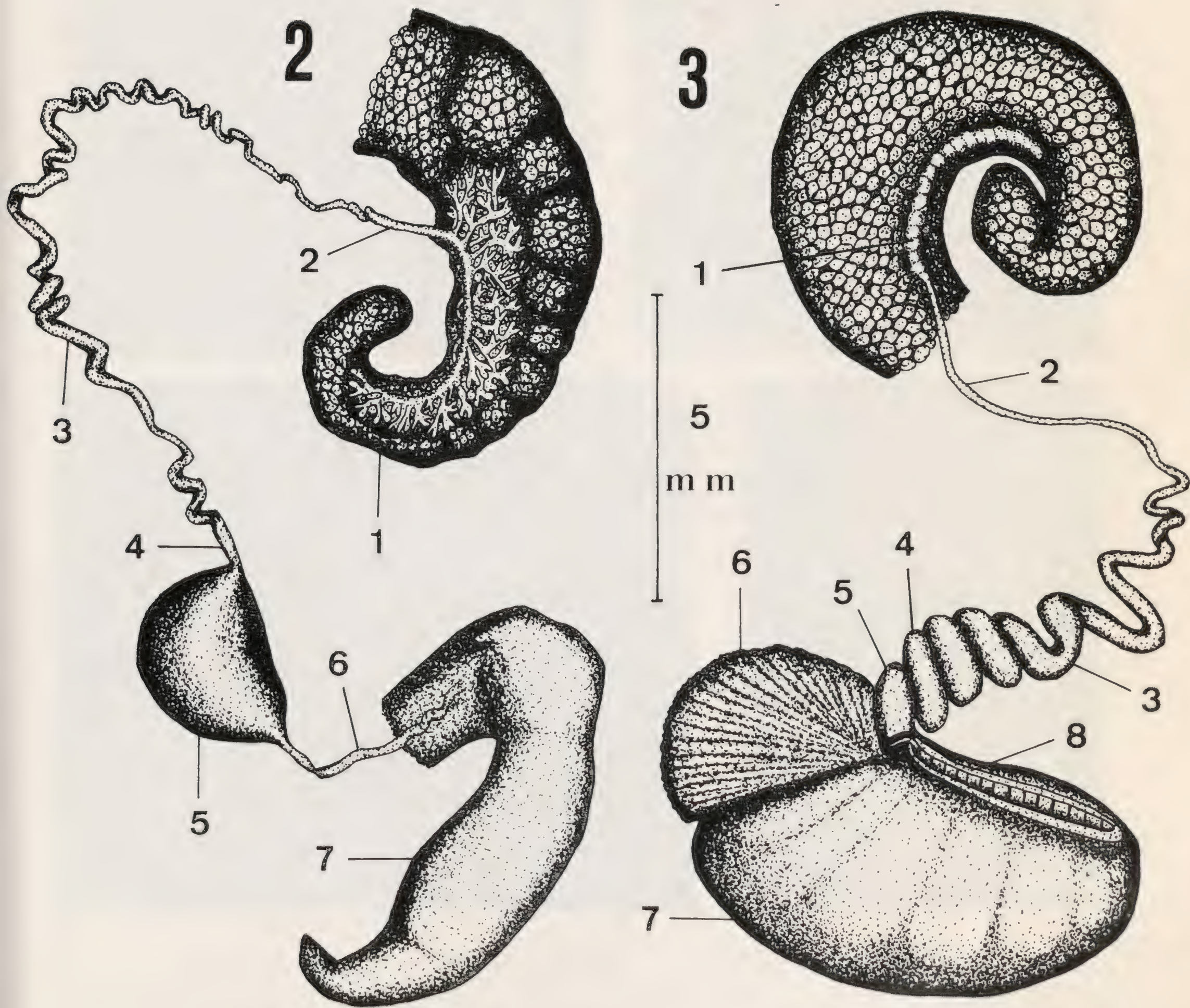
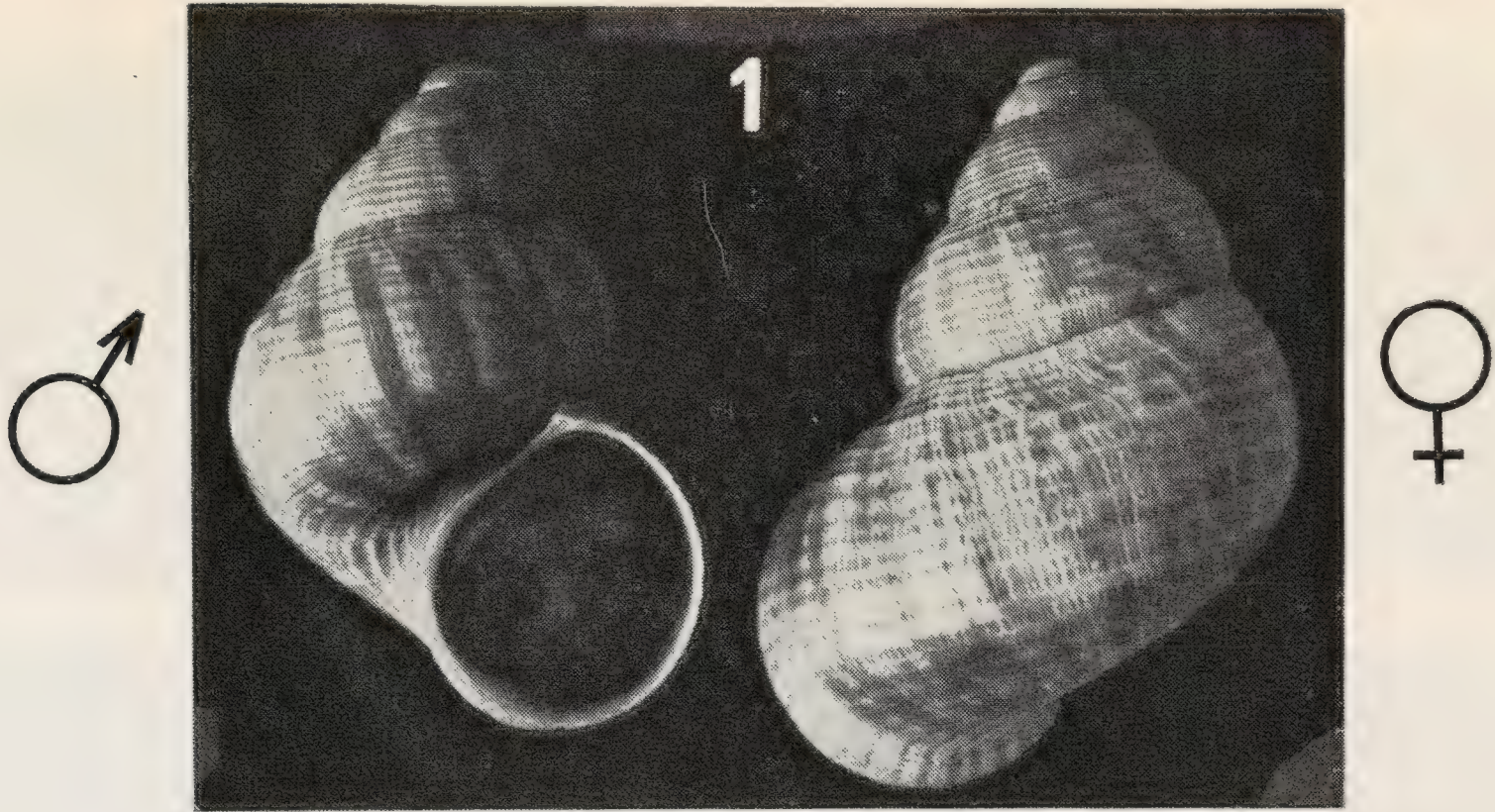


Plate 5

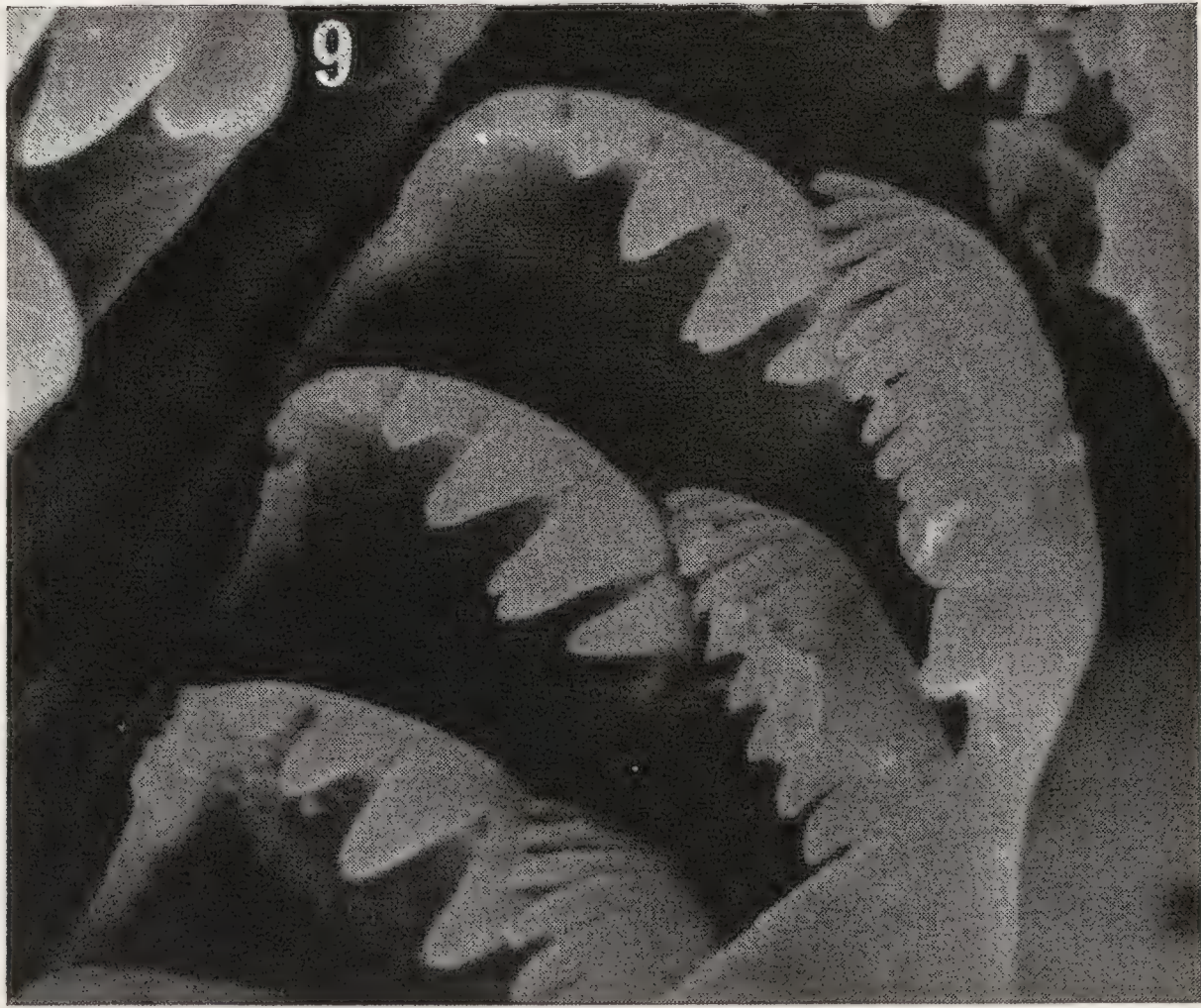
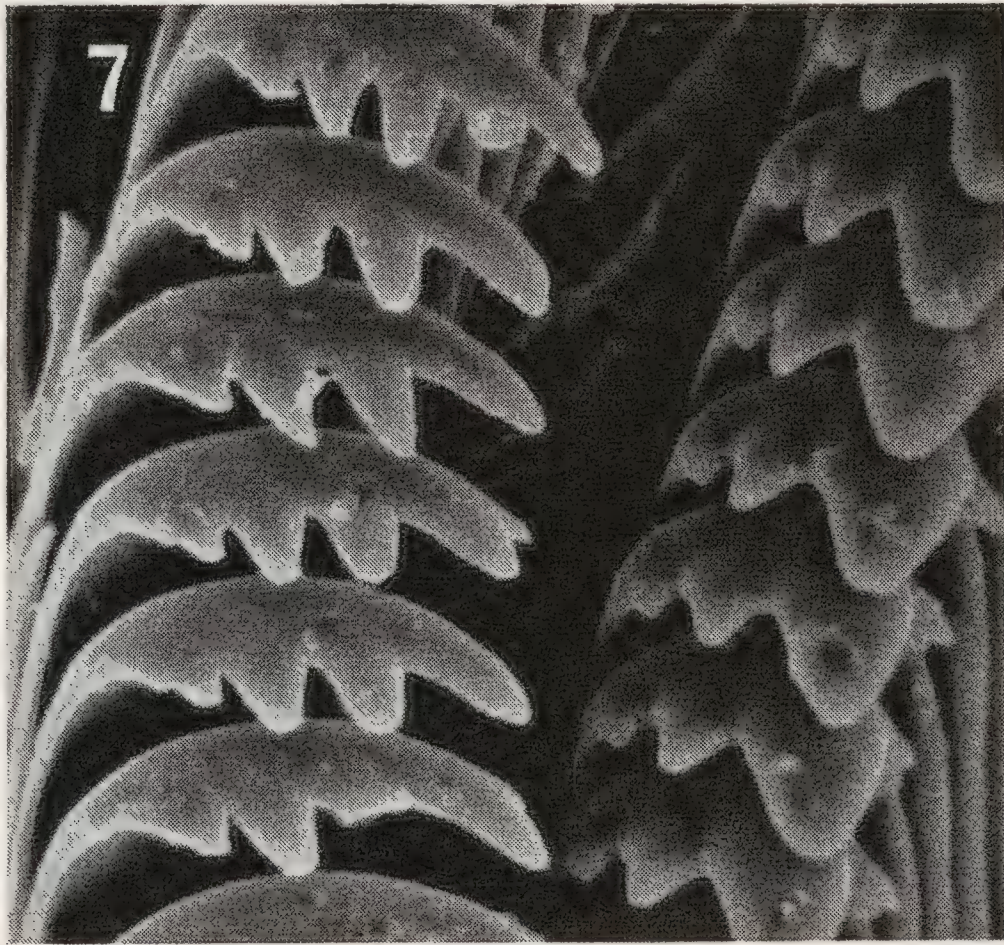
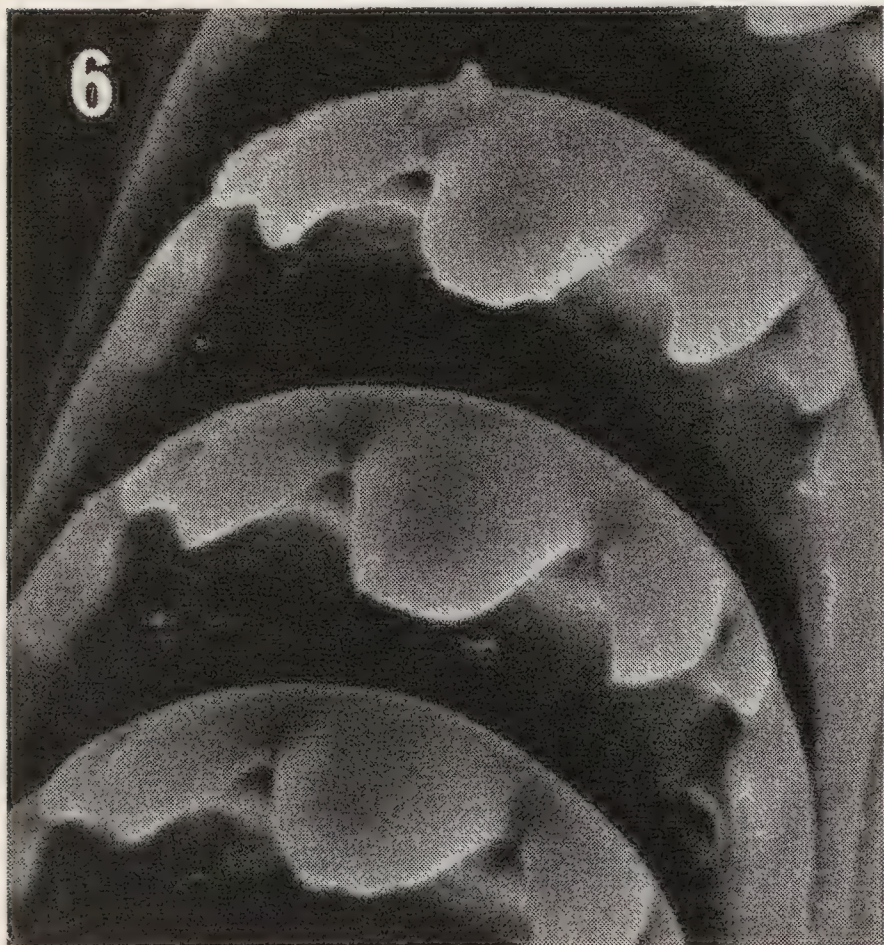


Plate 6

We have compared the shell, the genital system and the radula of *Pomatias sulcatus* with the shells of 2 populations of *Pomatias elegans* (one from Logroño, the other from Zaragoza, Spain), the genital system as presented by Creek (1951) and the radula illustrated by Giusti (1970). Concerning the shell, the main differences between the species are shown in Table 1.

TABLE 1

Comparisons between the shells of *Pomatias elegans* and *Pomatias sulcatus*

	Colour	Spiral Ridges	Peristome	Operculum	Dimensions (in mm)
<i>Pomatias elegans</i>	apex mauve: shell grayish or reddish with discontinuous bands, brown or violet-coloured	close and rather salient	not prominent	slightly inserted in the aperture (almost at the peristome)	10–18 height 8–13 width
<i>Pomatias sulcatus</i>	apex yellow; shell yellowish or orange-coloured with irregular bands, orange-coloured, very marked	widely spaced and only slightly salient	very prominent	deeply inserted in the aperture	17.6–23.5 height 12.5–14.4 width

We think that the sexual dimorphism is more evident in *Pomatias sulcatus* than in *Pomatias elegans*, but we cannot venture a definite conclusion, because our population of live specimens is very small.

Regarding the genital system, in *Pomatias sulcatus* it is larger than in *Pomatias elegans*; this is logical, because the specimens of *Pomatias sulcatus* are larger than the specimens of *Pomatias elegans*; notwithstanding, there are relative differences: see Table 2.

TABLE 2

Comparison between the genital systems of *Pomatias elegans* and *Pomatias sulcatus*

A: length of the male duct, from the testis to the prostate; B: length of the female duct, from the ovary to the receptaculum seminis; C: length of the prostate; D: length of the albumen gland plus the capsule gland; E: length of the female opening.

	A	A/B	A/C	B/D	B/E
<i>Pomatias elegans</i>	≈ 16 mm	≈ 2.2	≈ 7	≈ 1.3	≈ 2.1
<i>Pomatias sulcatus</i>	≈ 25 mm	≈ 1.2	≈ 8.3	≈ 2.4	≈ 5.4

Of the data shown in the above Table, the most remarkable is the difference in length between the male duct and the female duct in *Pomatias elegans*; this length is similar in both ducts in *Pomatias sulcatus*.

Lastly, in the radula the main difference between *Pomatias sulcatus* and *Pomatias elegans* is the greater number of denticles on each central and lateral teeth, and the smaller number of denticles in the marginal tooth of *Pomatias sulcatus*, as shown in Table 3.

Plate 6 (opposite)

Fig. 4. radula, general aspect, × 200. Fig. 5. central and first lateral tooth, × 500. Fig. 6. central tooth, × 1000. Fig. 7. first and second lateral teeth, × 500. Fig. 8. second lateral tooth, × 500. Fig. 9. marginal tooth, × 1000.

TABLE 3

Comparison between the radulae of *Pomatias elegans* and *Pomatias sulcatus*, concerning the number of denticles of each tooth.

	Central tooth	First lateral tooth	Second lateral tooth	Marginal tooth
<i>Pomatias elegans</i>	3	3	3-4	>20
<i>Pomatias sulcatus</i>	5-7	4	4-5	16-18

Futhermore, in *Pomatias sulcatus* the denticles of the central tooth are more separate and divergent. In the first lateral tooth of *Pomatias sulcatus*, the denticle is larger and rounded, while in *Pomatias elegans* it is sharp-pointed. In the second lateral tooth of *Pomatias sulcatus*, the denticles are more sharp-pointed than in *Pomatias elegans*. Finally, in the marginal tooth of *Pomatias sulcatus* the denticles are more separated than in *Pomatias elegans*.

ACKNOWLEDGEMENT

We should like to express our thanks to Dr. Forcart of Basel for his information about the anatomy of *Pomatias sulcatus*.

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ACTIVITY OF DIFFERENT SPECIES OF LAND-SNAIL ON SURFACES OF DIFFERENT INCLINATIONS

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Abstract: Observations on active snails at night give some support to the suggestion of Cain (1977) that there is a tendency for high-spired snails (other than burrowers) to prefer vertical surfaces when crawling, and for those with disc-like shells to prefer horizontal ones. Those with more-or-less globular shells show little preference. The absence or rarity of shells which are both tall and wide in most faunas may be due to a scarcity of surfaces of a rather narrow range of inclinations that would be appropriate to them. The overlap of more-or-less globular shells with both high-spired and disc-like ones is probably due to the preference of the globular ones for live herbaceous vegetation which is not favoured by the others.

Cain (1977) suggested tentatively that the bimodal distribution of land snail shell shapes found in several very different faunas might be related to preferred sites of activity, high-spired snails, except burrowers, walking and feeding by preference on more vertical surfaces, and equidimensional to flat-shelled ones preferring more horizontal surfaces. In the course of other field work in autumn 1977 the opportunity was taken to make a preliminary test of the hypothesis; as it was produced by A. J. C., all the observations were made by R. H. C. While a satisfactory test of it will require extensive observations in different places, at different times of the year, and on different faunas, these initial observations are of sufficient interest to report in the hope that others will extend them elsewhere.

DESCRIPTION OF SITES

Snails were observed at two localities: Woodchester Park, (National grid reference SO 810013), a privately owned valley in the Cotswolds four miles west of Stroud, Gloucestershire, and Tenby (SN 132001) on the Pembrokeshire (now Dyfed) coast, South Wales.

Woodchester Park:—

(1) A small disused limestone quarry in the valley. The ground was covered with small pieces of stone and limestone gravel derived from the crumbling vertical face of the quarry; there was sparse leaf litter from the hazel and brambles within the quarry and from trees growing at its top. Few herbaceous plants were present but some dead stems did provide a further alternative substrate for the snails.

(2) Two fallen tree trunks (diameter about 50 cm) and surrounding vegetation in woodland. They had fallen so as to lie horizontally between about 0.5 and 1.5 m above the ground. They were covered on one side by moss, and were bare on the other; in some places the bark had come away from the wood. The vegetation beneath them was largely grass and brambles, with but little bare soil and leaf litter.

(3) Various places alongside paths in deciduous woodland, according as snails were met with. At these sites there was plenty of bare soil and leaf litter with little live herbage at ground level. Vertical surfaces were supplied by frequent tree trunks, and by leaves on edge among the litter.

- (4) An area of thick lush grass beneath a very openly planted grove of poplars. Vertical surfaces were the trunks and some rough grass.
- (5) A pile of logs beside a track in woodland near the quarry, with grass, brambles and nettles growing around them.

Tenby:—

- (1) A narrow strip between the public gardens beneath the Esplanade and the edge of the vertical cliff down to the beach, with fairly typical cliff-top vegetation. An area $2\text{ m} \times 2\text{ m}$ was searched. The soil was extremely sandy, and the vegetation comprised dying sea beet (*Beta maritima*), buck's-horn plantain (*Plantago coronopus*), samphire (*Crithmum maritimum*) and some grass. A stone wall and stone steps bordered two sides of the site.
- (2) Rectory Field car park. A strip between the tarmac car park and the sloping path down to the beach. An area $2\text{ m} \times 2\text{ m}$ was searched. The vegetation was short grass and low plants (some *Plantago coronopus*) with newly growing alexanders (*Smyrnium olusatrum*). The sward was dense, leaving very little bare ground; some dead grass and other leaves were present.

At all sites there were alternative inclinations for any snail to choose from. (Since only a tendency is expected, it is quite likely that species with shells of any shape could live, if compelled by lack of choice, on a horizontal surface for example, but would then give no useful information for the present purpose).

METHODS

Snails were observed in the early evening soon after dark. A systematic search of each site was not carried out, but each microhabitat within each site was investigated. No part of the habitat was disturbed. When an active snail was found, a record was made of the type and inclination of the substrate it was on. The inclination was judged by eye. In such judging it is likely that one would tend to record some angles more frequently than others. In this case, angles of 0° for approximately horizontal surfaces, 30° for gently sloping ones, 45° for those clearly close to halfway between 0° and 90° , 60° for steeper ones, 80° for very steep ones, and of course 90° for vertical ones, and corresponding ones for overhanging surfaces, were usual. The angles are so grouped in this paper that these biases are unlikely to affect the results.

The diagrams in Cain (1977) of distribution of height of shell (h) against maximum diameter (d) show that high-spined shells tend to have values of h/d from about 4.0 to 2.0. The data on which these were based were taken from Germain (1930–1) and are used again here. For equidimensional shells $h/d = 1$, and there is a continuous scatter thence of lower values down to about 0.3. The species mentioned in the present paper fall into groups with values from 4.2 to 2.5 (high-spined shells), a single species, *Pomatias elegans*, at 1.3, a group of more or less globular ones from 0.8 to 0.75, and another of definitely flattened ones from 0.56 to 0.40. *P. elegans* is included here with the high-spined shells, so that three groups are recognized (see below for a list of constituent species).

On three occasions *Clausilia bidentata*, and on two *Discus rotundatus*, were found in the act of crawling into or emerging from a small crevice; as their angles of inclination could not be determined, these observations only have been omitted.

OBSERVATIONS

The observations are given in Table 1. If we group them into five equal intervals (0° to 36° , 37° to 72° , etc.) and group the species as high-spined (*Abida secale*, *Cochlodina laminata*, *Clausilia bidentata*, *Azeca goodalli*, *Pomatias elegans*, *Cochlicella acuta*), more or less globular (*Cepaea hortensis*, *C. nemoralis*, *Helix aspersa*, *Theba pisana*, *Cernuella virgata*) and flattened ones (*Trichia striolata*, *Oxychilus cellarius*, *O. alliarius*, *Discus rotundatus*), we obtain Table 2. Combining the last three

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TABLE 1.
No. of individuals moving on various inclinations of substrate

Species	0°-20°	21°-36°	37°-45°	46°-72°	73°-108°	109°-144°	145°-180°
Woodchester							
<i>O. alliarius</i>	1						
<i>O. cellarius</i>	4			1	1		
<i>T. striolata</i>	2						
<i>D. rotundatus</i>	5		1		1		
<i>C. hortensis</i>	1						
<i>C. nemoralis</i>				1	1		1
<i>A. arbustorum</i>	1				1		
<i>P. elegans</i>			1				
<i>A. secale</i>				1			
<i>C. laminata</i>	1	1		1			
<i>A. goodalli</i>	1						
<i>C. bidentata</i>	3	1			11	1	2
Tenby							
<i>C. virgata</i>	5		2	1			
<i>T. pisana</i>	4		2	3	3	2	5
<i>H. aspersa</i>					1		
<i>C. acuta</i>			1	2			

TABLE 2.
Distribution of shells of different shape in relation to inclination of substrate, when the snails are active

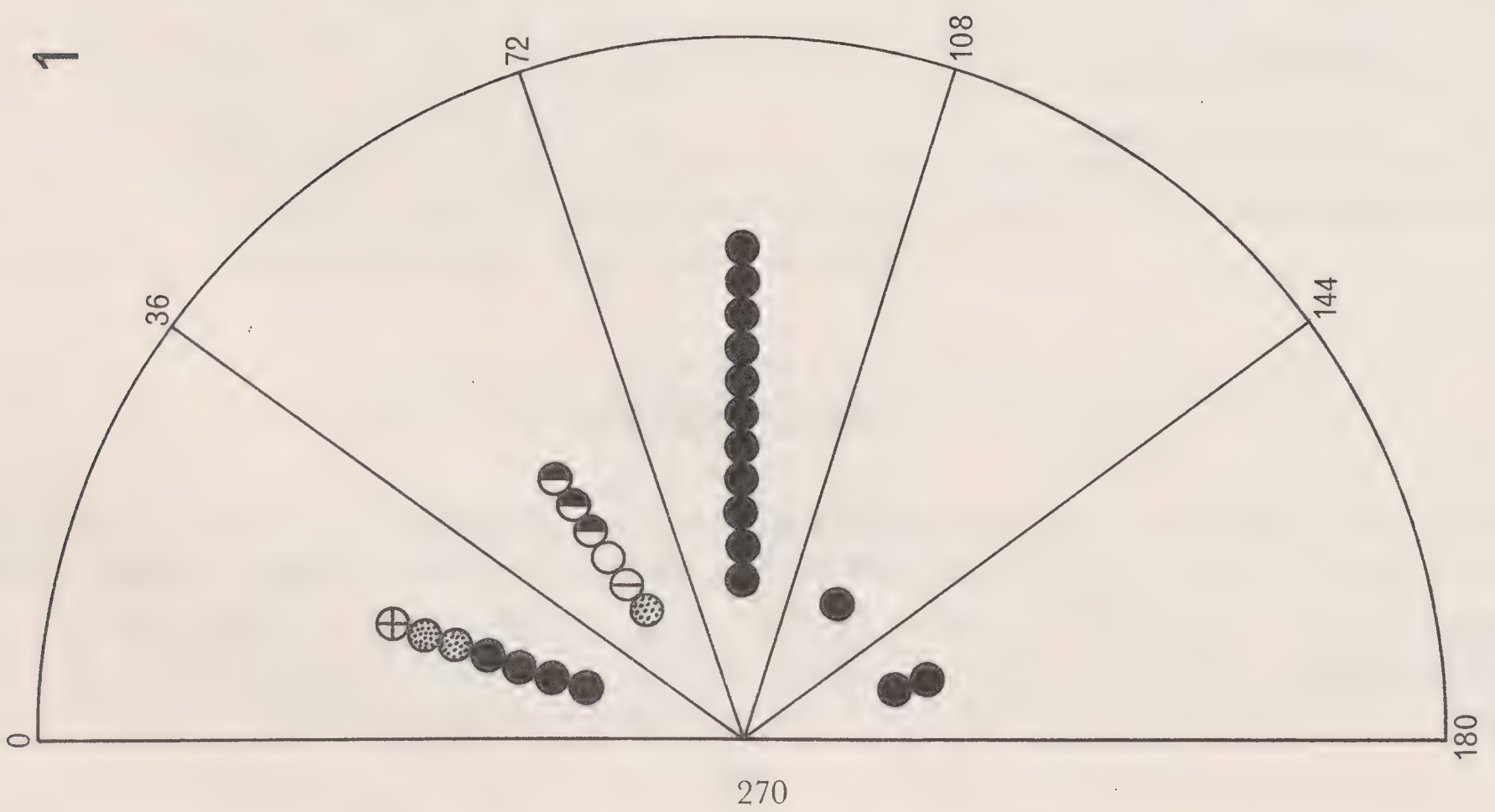
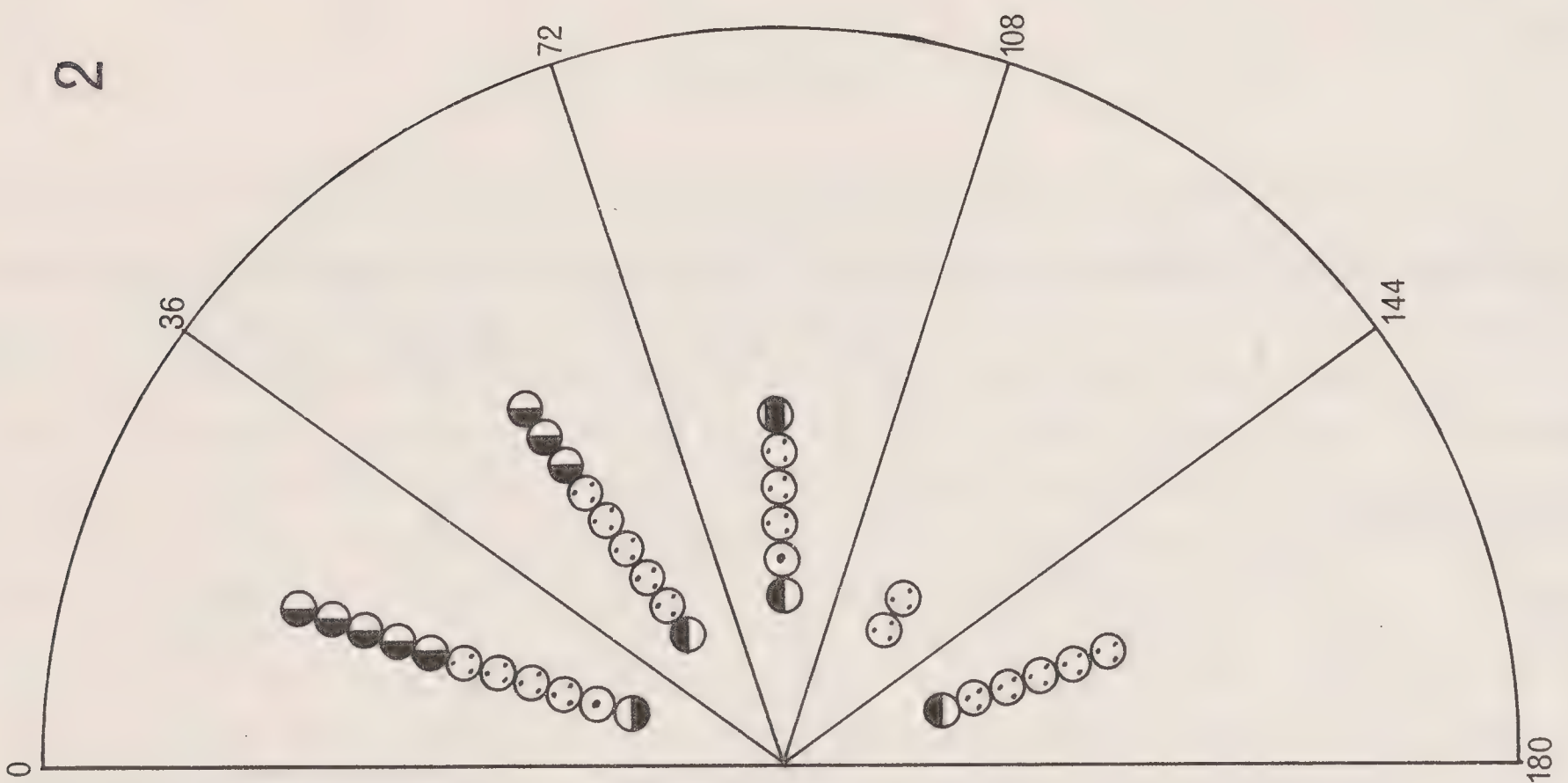
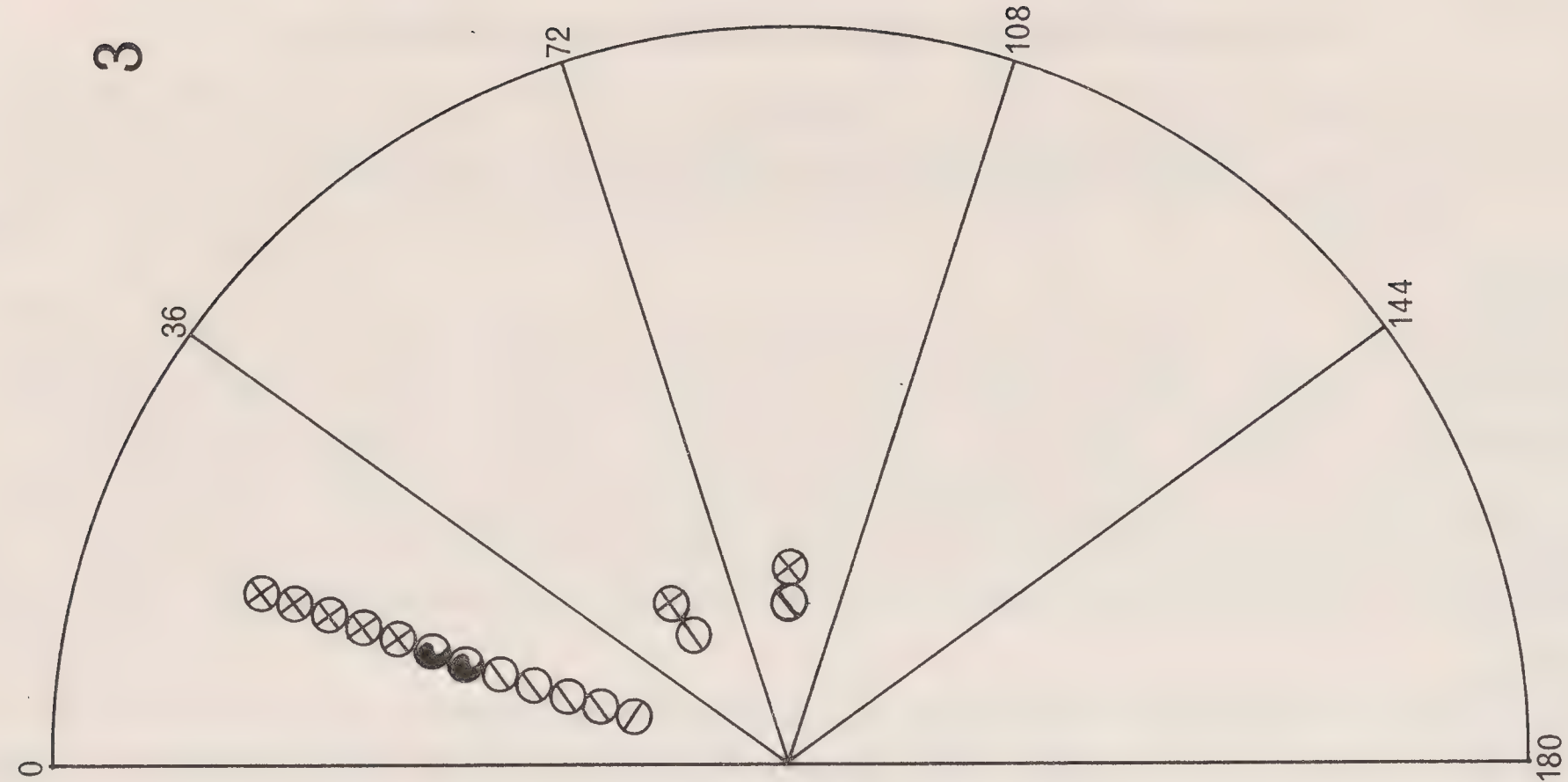
	0°-36°	37°-72°	73°-108°	109°-144°	145°-180°
high-spired	7	6	11	1	2
more-or-less globular	11	9	6	2	6
flattened	12	2	2	0	0

TABLE 3.
Data in Table 2 regrouped into intervals probably more meaningful biologically

	0°-20°	21°-45°	46°-180°
high-spired	5	4	18
more-or-less globular	11	4	19
flattened	12	1	3

TABLE 4.
Observations of active snails on different types of substrate

	Live herbaceous plants	Dead herbaceous stems	Wood or bark	Stone	Soil	Leaf litter
high-spired	2	0	21	2	1	1
more-or-less globular	22	6	1	0	2	3
flattened	1	0	5	0	5	5



columns to get adequate expectations, this gives χ^2 (d. f. 4) = 11.9, P between 0.02 and 0.01. Inspection shows that the largest single contribution to this value is a close association of flattened shells with horizontal surfaces. The distributions in each row of Table 2 are shown diagrammatically in Figs. 1, 2 and 3 with the species symbolized, and it is clear that this association (Fig. 3) is not due to one single species. The other noticeable contributions come from a deficiency of high-spined shells on horizontal surfaces and a surplus on vertical ones, and a deficiency of flattened ones on vertical to overhanging surfaces. While all the high-spined shells on vertical surfaces are of *Clausilia bidentata*, the species is not confined to them, and other high-spined species are on strongly sloping surfaces (Fig. 1).

If, as the hypothesis suggests, high-spined shells, which are stable when hanging vertically, are associated with more vertical surfaces, then actually overhanging ones should be counted with verticals, and so there is some biological justification for combining the last three columns of Table 2. But we do not know at what angle of inclination a species with a flattened shell begins to feel uncomfortable; a comparatively slight slope might be sufficiently different from a horizontal one if the shell then tended to slip down it. Accordingly, we can regroup the data in Table 1 as in Table 3. This actually increases the differences between the rows, with high-spined shells predominantly at angles of 45° or more, and flattened ones at 20° and less. The more globular shells in both tables seem to show little preference. The numbers in the central column of Table 3 are too small for adequate expectations; if it is combined with the left-hand column χ^2 (d. f. 2) is 9.62, if with the right-hand one, it is 14.27, both times with the probabilities greater than for Table 2.

DISCUSSION

Although the data are scanty, they indicate considerable differences in preferred angle of inclination in association with shell shape, rather than with species. In general, high-spined species prefer steeply sloping surfaces, those with flattened ones are strongly associated with horizontal or near-horizontal ones, and more globular-shelled species are distributed indiscriminately. A regrouping into surfaces of inclination 0 to 20°, 21 to 45°, and 46 to 180° seems to indicate sharper differences between the shape classes. With more data, it may be possible to determine the preferences more clearly and define a critical angle or range for the changeover from flattened to high-spined shells. It is probably only an amusing coincidence that the single observation for the species that could be considered both tall and broad-shelled (*Pomatias elegans*) is of it crawling on stone at 45°; nevertheless, if tall narrow shells are found from 180° to about 45°, and flattened ones from 0° to 20° or more, it is worth asking whether the range of inclinations appropriate to a tall and broad shell is not too narrow or too seldom exemplified in European habitats to afford a niche for such species.

The second main indication from these data is that more or less globular shells are found rather indiscriminately at inclinations from 0° to 180°, and therefore overlap in distribution with both the flattened and the high-spined shells. When the data available here are grouped according to substrate as in table 4, a highly significant preference by globular shells but not the

Fig. 1. Distribution of high-spined species observed when active, with respect to angle of inclination of the substrate, from 0° (horizontal) through 90° (vertical) to 180° (snail on horizontal undersurface). Black circles, *Clausilia bidentata*; stippled, *Cochlodina laminata*; right-hand half black, *Cochlicella acuta*; cross, *Azeca goodalli*; vertical line, *Pomatias elegans*; plain circle, *Abida secale*.

Fig. 2. Distribution, as in Fig. 1, for more-or-less globular-shelled species. Circle with three dots, *Theba pisana*; with broad black horizontal stripe, *Helix aspersa*; upper half black, *Cepaea nemoralis*; lower half black, *C. hortensis*; with central spot, *Arianta arbustorum*; left-hand half black, *Cernuella virgata*.

Fig. 3. Distribution, as in Fig. 1, for species with flattened shells. Circle with St. Andrew's cross, *Discus rotundatus*; oblique line sloping down to left, *Oxychilus cellarius*; oblique line sloping down to right, *O. alliarius*; yin and yang sign, *Trichia striolata*.

other classes for live herbaceous plants, is found, although the data are almost entirely from two species, *Theba pisana* and *Ceriuella virgata*. Those species with high-spined shells are mainly woodland or rock-dwelling species, and those with flattened shells are usually on litter or soil when active. It is our experience that such species as *Cepaea hortensis* and *C. nemoralis* and *Arianta arbustorum* are heavily associated with growths of herbaceous plants along woodland rides, at edges of woods, in hedgerow edges with banks of weeds, and among broad-leaved herbs in open grassland; they are only occasionally or sparsely deep woodland species. In climbing amongst herbs they may occur on the stems or leaves or dead stems at any angle of inclination. It is probable, therefore, that there is not much overlap ecologically between them and species with flattened or high-spined shells (which equally will not overlap when active), but this point needs further investigation with respect to such species as *Trichia striolata* and *Monacha cantiana*. We need to know whether these two prefer more horizontal surfaces than *C. nemoralis*, for example, and whether the large number of species with moderately flattened shells (Cain, 1977) are those which, although climbing often, spend most of their active time (not all) on more or less horizontal surfaces.

It must be remembered that under certain weather conditions, when the ground surface becomes very hot or wet, all species may have to climb; we are looking only for tendencies. Thus on occasion *Cepaea* species may be seen many feet up tree-trunks. Nevertheless, they cannot be classed as tree snails.

It is hoped that this preliminary note will show the interest of and necessity for such studies.

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DIFFERENCES IN THE SITES OF ACTIVITY OF COEXISTING SPECIES OF LAND MOLLUSC

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Abstract: Nocturnal observations of the activity of land molluscs at four locations (three open and rocky, one wooded), show that there are substantial differences in the sites of activity of some species living in the same place. Vertical and horizontal rock faces, bare soil, living and dead vegetation, tree trunks and fallen logs all have characteristic species. The sites of activity of snails are related to shell shape, with the tallest preferring hard vertical surfaces and the most flattened, bare soil. Such differences help, in a limited way, to account for the diversity of species found in some habitats.

Both the coexistence of many species of land mollusc in a single habitat, and the wide range of habitats occupied by many species, can be explained at present only in the most general terms, in relation to climate, shelter and lime (Boycott 1934, Cameron and Redfern 1972). Some differences in the diets of coexisting species have been demonstrated, but these are usually slight and not always consistent from place to place (Mason 1970, Chatfield 1975, Carter, Jeffery and Williamson in prep.). Feeding is selective, but polyphagous and opportunistic; absolute shortages are probably rare (Mason 1970, Williamson 1975,) but densities are often higher when one food plant is particularly abundant (Cain and Currey 1968, Grime and Blythe 1969, Carter *et al.* in prep.). Differences in the behaviour of coexisting species have occasionally been demonstrated in the field and in the laboratory (Cameron 1970a, b, Johnson and Lowy 1948), but in general, evidence for such distinctions is scattered and anecdotal.

Cain (1977) has opened up a new approach to this problem by showing that most modern snail faunas have a distinctly non-random distribution of shell-shapes, with tall and flattened forms being more abundant than the intermediate globular ones. The terrestrial snail fauna of western Europe fits this pattern.

This dichotomy in shell shapes does not correspond to the broad ecological deployment of the species concerned; tall and flattened forms are found together in most habitats (Cain 1977). Cain suggested, on mechanical grounds, that it might correspond to specific differences in sites and modes of activity, but he could find no quantitative evidence to test this idea. This paper presents the results of a field study on the sites of activity of species living in the same place, and relates them both to the general problem of coexistence, and to the shapes and sizes of their shells.

STUDY SITES AND METHODS

The work was carried out at four study sites in the immediate vicinity of Malham Tarn Field Centre, Settle, N. Yorkshire (National Grid Reference SD 894673), on four successive nights in August 1977. Details of each study site are given below.

1. Highfolds Scar. An area of small limestone crags in heavily grazed grassland. The crags form low broken vertical ridges, between which are flatter areas of grass and loose rock, with some bare soil. Herbaceous plants are mostly small rosette-forming species living in the grass sward.
2. The Holmes Rockery. A natural outcrop of limestone in tall ungrazed vegetation, partially overhung by small bushes. The area includes an earth path and steps made of concrete paving slabs. Vegetation mostly more than 20 cm. high.
3. Driveway cliffs and wall. A line of small man-made cliffs and stone retaining wall alongside the drive going round the back of the Field Centre, and including a narrow flat strip of soil and vegetation at the base. Dog's mercury, *Mercurialis perennis*, is the dominant herb, with some ivy, *Hedera helix*, on the cliffs. The area is overhung by the trees of Tarn House Wood.
4. Tarn House Wood. A small strip of this wood adjacent to a path leading from the Field Centre to the summit of Highfolds Scar. There is a moderate slope (10–20°) with only a few exposed rocks, mostly well bedded into the soil. There are many fallen trunks and branches. The commonest tree is sycamore, *Acer pseudoplatanus*, but many others are present. The ground flora is mostly *Mercurialis perennis*, with patches of bramble and raspberry, *Rubus* spp. Much bare soil and litter is visible.

Each site was searched by torchlight on one night between 21.30 and 23.30 hours. The weather was similar on all occasions—warm and damp, with light winds and occasional drizzle. All exposed rock and soil surfaces were wet. Every active slug and snail seen was scored for species and position, each area being traversed systematically to avoid encountering the same animals again. The habitat was not disturbed, but the undersides of leaves and bare soil under vegetation were searched as far as possible.

In sites 1–3, there were four common and easily scoreable microhabitats—vertical rock faces, horizontal rock faces (nearly all facing upwards), bare soil, and living vegetation. The distinction between the first two is arbitrary, being taken as 45°, but the configuration of the rocks made them easy to score in most cases. In site 4, the vertical rock category was very rare, and the two snails seen on it have been ignored. Three additional microhabitats were found here—fallen logs, living tree-trunks and dead plants (usually prostrate, but more or less intact). No attempt was made to estimate the relative amounts of each kind of microhabitat searched. Analysis therefore compares species within each site; direct comparisons of the results for one species between sites are not possible.

RESULTS

The numbers of each species recorded in each habitat in each site are shown in Table 1. Only species recorded at least ten times in one site are included. Others were seen in small numbers in one or more sites. It can be seen that there are substantial differences in the proportions of species seen active in different micro-habitats, and that most of these differences are consistent from site to site. It is difficult to test the significance of the overall distributions in each site, because there is a large number of expected values of less than five (Campbell 1967). Individual comparisons of pairs of species, however, reveal many significant differences in distribution.

In sites 1, 2 and 3, three categories of species can be recognized:—1) those preferring rocks (horizontal and vertical combined): *Clausilia dubia*, *C. bidentata*, *Pyramidula rupestris*, *Lauria cylindracea*, *Limax marginatus* and *Discus rotundatus*, of which only the last was ever found off rocks; 2) those preferring bare soil: *Oxychilus cellarius* and *Vitrea contracta*, and 3) those preferring living vegetation: *Trichia striolata* and *Arion ater*. The habitat distribution of each species in each group has been compared with that of each species in the other groups, and tested for significance (Table 2). The overwhelming majority of comparisons are highly significant.

There are also significant and consistent differences between members of the rock-dwelling group in their distribution between vertical and horizontal rocks. Table 3 shows the test results for all possible comparisons. *C. dubia* is restricted to vertical rocks; *C. bidentata* and *P. rupestris* occur rarely on horizontal rocks as well, but do not differ significantly from *C. dubia*. *D. rotundatus*

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TABLE 1

	Vertical rocks	Horizon- tal rocks	Bare soil	Green vege- tation	Dead vege- tation	Fallen logs	Tree trunks
Site 1.							
<i>Clausilia dubia</i>	13	0	0	0			
<i>Clausilia bidentata</i>	56	6	0	0			
<i>Pyramidula rupestris</i>	390	41	0	0			
<i>Lauria cylindracea</i>	69	38	0	0		not represented	
<i>Discus rotundatus</i>	3	15	1	0			
<i>Oxychilus cellarius</i>	0	0	14	0			
<i>Vitrea contracta</i>	0	0	10	0			
<i>Trichia striolata</i>	0	0	1	9			
<i>Arion ater</i>	0	0	1	12			
Site 2.							
<i>Clausilia dubia</i>	34	0	0	0			
<i>Clausilia bidentata</i>	9	1	0	0			
<i>Lauria cylindracea</i>	32	16	0	0			
<i>Discus rotundatus</i>	51	177	6	0		not represented	
<i>Oxychilus cellarius</i>	0	0	7	0			
<i>Vitrea contracta</i>	0	0	4	0			
<i>Trichia striolata</i>	2	3	2	15			
<i>Arion ater</i>	0	1	2	5			
Site 3.							
<i>Clausilia dubia</i>	48	0	0	0			
<i>Discus rotundatus</i>	30	13	1	0			
<i>Oxychilus cellarius</i>	0	0	11	0		not represented	
<i>Vitrea contracta</i>	0	1	5	0			
<i>Trichia striolata</i>	3	8	6	22			
<i>Arion ater</i>	0	1	3	10			
<i>Limax marginatus</i>	12	0	0	0			
Site 4.							
<i>Discus rotundatus</i>		29	2	0	4	45	2
<i>Oxychilus cellarius</i>		1	28	0	3	1	0
<i>Vitrea contracta</i>		0	4	0	0	1	0
<i>Trichia striolata</i>		1	6	14	20	1	0
<i>Arion ater</i>		0	2	12	4	4	0
<i>Limax marginatus</i>		1	0	0	0	2	29

The numbers of active individuals of each species seen on each habitat component of each site. Nomenclature in this table, and for all other species mentioned in the text, follows Waldén (1976).

TABLE 2

	Species predominating on rock			Species predominating on soil		
	Site	No.	Probability	Site	No.	Probability
Species predominating on soil	1	10	all <0.001			
	2	8	all <0.01			
	3	6	all <0.01			
Species predominating on green plants	1	10	all <0.001	1	4	all <0.001
	2	8	all <0.001	2	4	all but one <0.05
	3	6	all <0.001	3	4	all <0.02

Significance test results of all possible species comparisons between species predominating in different microhabitats for sites 1, 2 and 3.

No. = number of comparisons tested. All based on 2 × 2 contingency tables, with appropriate correction when expected values are less than 5.

shows a relative preference for horizontal rocks, while *L. cylindracea* is intermediate, but significantly different from both extremes. *L. marginatus* was restricted to vertical rocks in site 3.

Site 4 shows a similar picture. In the three habitat categories present also in sites 1–3 (rock, soil and living plants), the same trends can be seen, with *D. rotundatus* predominating on rock, *T. striolata* and *A. ater* on living plants and *O. cellarius* and *V. contracta* on soil. All these differences are significant ($P < 0.05$) except for a few involving *V. contracta*, whose numbers are low. Of the other habitats, fallen logs have a distribution of species similar to rocks, and living tree trunks hold little except *L. marginatus*. Dead plants hold the highest proportion of *T. striolata*, and the distributions of *T. striolata* and *A. ater* on living and dead plants are significantly different ($P < 0.05$).

DISCUSSION

The results show that there are substantial differences in the sites of activity of some species living in the same place, and that these differences tend to be consistent from one place to another. Impressions formed while sampling these and other similar sites nearby in daytime suggest that the differences in resting sites are much less. All these species, with the exception of *L. marginatus*, may be found sheltering under and round the same stone. Intensive daytime collecting also indicates that most of the species known to live in these sites were seen active. The most conspicuous exceptions, not due simply to rarity, are *Carychium tridentatum*, which is very small, and *Cochlicopa lubrica* and/or *lubricella*. The latter may be found in some numbers in daytime under logs and stones and at the base of grasses. Its absence may suggest a subterranean mode of activity, or one in the interstices between vegetation at ground level, not visible without disturbing the habitat.

One must be cautious in drawing conclusions from these results, because they relate to a single occasion in a few localities. Results obtained at different times of year, in different weather conditions, or in other areas might be different, and the contrast between sites 1–3 and site 4 emphasizes that results also depend on the range of microhabitats available. Nevertheless, these results are likely to be repeatable in the same general area: the rock-dwelling group are found wherever there are rocks, but not elsewhere, except for some, such as *D. rotundatus* and *L. marginatus* which are also found where logs or trees provide an alternative. Similarly, *A. ater* and *T. striolata* are missing from those habitats lacking higher plants—bare screes and rock rubble (Cameron and Redfern 1972, Cameron in prep., Evans and Jones 1973).

Differences in sites of activity of the sort shown here may help to account for the diversity of species found in any one site. Habitats in Britain with the greatest variety of such sites have very rich molluscan faunas, provided general conditions (e.g. moisture and soil calcium) are favourable (Boycott 1934, Cameron and Redfern 1972, Cameron 1973). Such differences in places of activity or feeding have often been found in other groups of animals (e.g. birds; Lack 1971) and form part of the evidence that closely related species living in the same place avoid interspecific competition by divergence in behavioural and anatomical characters relating to the resource in short supply. At present, the evidence presented here cannot be so used, for amongst the very limited range of species studied there are several with apparently similar activity sites. *Oxychilus cellarius* and *Vitrea contracta* appear identical, and in the three open sites so do *Arion ater* and *Trichia striolata*, and four rock-dwelling species are similarly indistinguishable—*Clausilia bidentata*, *C. dubia*, *Pyramidula rupestris* and *Limax marginatus*. In most of these cases there are substantial differences in size and shape between species, which might represent different forms of character divergence, but this is much less marked in the comparison of the two *Clausilia* species. In the British terrestrial snail fauna there are many pairs and sometimes threesomes of closely related species of similar size and shape which may be found together. If this *Clausilia* pair is typical, differences in sites of activity may be slight.

TABLE 3

	<i>Clausilia dubia</i>	<i>Clausilia bidentata</i>	<i>Pyramidula rupestris</i>	<i>Lauria cylindracea</i>
Site 1.				
<i>Clausilia bidentata</i>	NS			
<i>Pyramidula rupestris</i>	NS	NS		
<i>Lauria cylindracea</i>	<0.01	<0.001	<0.001	
<i>Discus rotundatus</i>	<0.001	<0.001	<0.001	<0.001
Site 2.				
<i>Clausilia bidentata</i>	NS			
<i>Lauria cylindracea</i>	<0.001	NS		
<i>Discus rotundatus</i>	<0.001	<0.001	<0.001	
Site 3.				
<i>Limax marginatus</i>	NS	<i>Limax marginatus</i>		
<i>Discus rotundatus</i>	<0.001	NS		

Significance test results for distribution of rock dwelling species between vertical and horizontal surfaces, for sites 1, 2 and 3. NS = not significant, $P = 0.05$.

The evidence suggests that it is the structure, shape or texture of the substrate, rather than its composition, which is important. Vertical tree trunks are an alternative to rocks for *L. marginatus*, and many species are common to woody and rocky surfaces generally. Only *P. rupestris* of the species found on rocks here is confined to them throughout its range—even *C. dubia* occurring in rockless woodland in continental Europe (Adam 1960, Favre 1927). Differences in preferences for size and shape of surface on which to climb have been demonstrated for two species by Johnson and Lowy (1948).

Cain (1977) has suggested that shell shape, which is not connected to the broad habitats of snails, may relate to site of activity. This study tends to confirm this. Three species here are clearly taller than they are broad—the *Clausilia* species and *L. cylindracea*. All are rock dwellers, and with a relative preference for vertical surfaces. *L. cylindracea* is shorter in relation to its breadth than *Clausilia*, and is more frequently found on horizontal surfaces, while the flattened *D. rotundatus* predominates on them. The largely horizontal soil surface also supports flattened species: *O. cellarius* and *V. contracta*. The significant exception in this sequence is *P. rupestris*—flattened, but on the evidence as fond of vertical surfaces as *C. bidentata*. If discoidal shells are at a disadvantage on vertical surfaces because of the muscular effort needed to keep them correctly aligned (Cain 1977), it is possible that the small size of *P. rupestris* partly offsets this, as the force per unit weight exerted by small animals is usually greater than by large (Alexander 1971). If this is so, juveniles of discoidal species might be expected to frequent vertical surfaces more often than adults.

If tall shells relate to climbing vertical surfaces, and perhaps also to burrowing—cf. *Cochlicopa* above and Cain's (1977) comments on *Cecilioides acicula*, and discoidal shells to firm horizontal surfaces, where do the globular species fit in? *T. striolata* is not completely globular, but is less flattened than the species found on horizontal surfaces; it was found most often climbing on herbaceous vegetation. *T. striolata* and the more globular *Monacha cantiana* certainly eat living plants, including flower heads, and presumably climb the plants to do so (Châtfield 1975). The very globular *Helix aspersa* is the only serious snail pest of horticultural crops, and the globular *Cepaea nemoralis* and *Arianta arbustorum*, although usually eaters of decaying plant matter (Williamson and Cameron 1976) ascend plants to feed on senescent leaves some distance from the ground (Grime and Blythe 1969). Flattened helicids of similar size are rare in Britain, but *Helicodonta obvoluta* lives on logs in woodland (Cameron 1972) and *Helicigona lapicida* on rocks and also again in woodland (Ellis 1969). Herbaceous plants present surfaces of a variety of

angles and shapes; they are also unstable, moving in the wind, and when a snail moves over them. A globular shell, particularly if attached to a broad foot and pedicel (Cain 1977) may be the most suitable structure for this perilous site.

ACKNOWLEDGEMENTS

I wish to thank Professor A. J. Cain for criticism of a draft of this paper, Dr. M. A. Carter for access to unpublished material, and Dr. R. H. L. Disney for facilities at Malham Tarn Field Centre.

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OBITUARY

OBITUARY

Charles Theodore Cribb, 1888-1976.

It is with some humility that I pay tribute to a friend who influenced me considerably in my early conchological days and who gave me, a beginner, every encouragement and the run of his collection and library. The first time I encountered Canon Cribb was in 1959 soon after my joining the Conchological Society when I had the fortune to visit him at the Vicarage at Moseley, some half mile from my home. We met at about 8.30 p.m. and during our half an hour encounter he, besides showing me his extensive collection of Javanese and New Zealand land and freshwater Mollusca, also carried out his pastoral duties by arranging two christenings and a wedding. Future meetings followed the same pattern, the vicarage being an open house, but at no time can I remember him being too busy to see anyone or assist in any problem, but his every spare moment was spent with his molluscan collections which were primarily amassed by his own efforts in the field.

C. T. Cribb was born at Stepney, London on October 6th, 1888, his father being vicar at St. James's Church Stepney, whence the family moved to Yorkshire during his early childhood. He was educated at Bradford Grammar School and whilst there developed a close friendship with Richard Eric Mortimer Wheeler, later Sir Mortimer Wheeler, the eminent archaeologist, who was known at school as "Remy". During their association at Bradford Grammar School the duo were responsible for the production of the fifth form magazine. "Remy" wrote, typed and did all the illustrations for the school magazine although he attributed it to "Byron" (nickname of C. T. Cribb given him by his Mathematics master, Mr. Jones). The names R. E. M. Wheeler and Chas. T. Byron are the signatories of a letter in the magazine and it is followed by a letter starting "Dear Cribb". The name of Wheeler is in one or two other places. One issue of the magazine is inscribed "To Theodore". In actual fact C. T. Cribb or "Byron" was the Business Manager. Only one copy of each issue of the magazine was produced and the Business Manager circulated it from one boy to another—each boy (or master) was allowed to keep the magazine for twenty four hours on payment of 1d. This magazine was referred to by Mortimer Wheeler in his autobiography but he made no mention of "Byron". Two issues of this magazine remain in the possession of C. T. Cribb's son and an illustration by "Remy" from this magazine depicting him is illustrated herewith.

On leaving school, he took a job in the Bank of Liverpool (later to become Martins Bank) at Skipton, Yorkshire. During this period prior to the outbreak of the 1914-18 war, C. T. Cribb lectured frequently in the north of England on 'The Life and Work of Insects' and 'The Life of the Mollusca'. He had always wanted to follow his father into the Church and in 1914 he entered Durham University but in 1915 left to volunteer for the services, joining the Army Service Corps with which Company he was stationed at Audruicq, France. Whilst there he actively collected the local land and freshwater Mollusca during lulls in the fighting, this material being sent home to J. W. Taylor who published the results for him in the *Journal of Conchology*, Volume 16, 1920, under the title 'The Land and Freshwater Molluscs of Audruicq, Pas-de-Calais'. Taylor states that "Lieut. C. Theodore Cribb, who was stationed at Audruicq, near St. Omer, during 1916, availed himself of his scanty opportunities to make a collection of the mollusks to be found within a radius of four or five miles of that place; these results being supplemented by an occasional visit to Calais. In 1838 Bouchard-Chantreaux published an excellent treatise upon the mollusks of the Pas-de-Calais, the only one ever published for this department, in which he enumerated 102 species, but after deducting those species which are halophilous and others which are now regarded as varieties, this number may be reduced to 85. Lieut. Cribb found 55 species, which must be regarded as a gratifying result, more especially as six species are additional to those cited by Bouchard-Chantreaux".

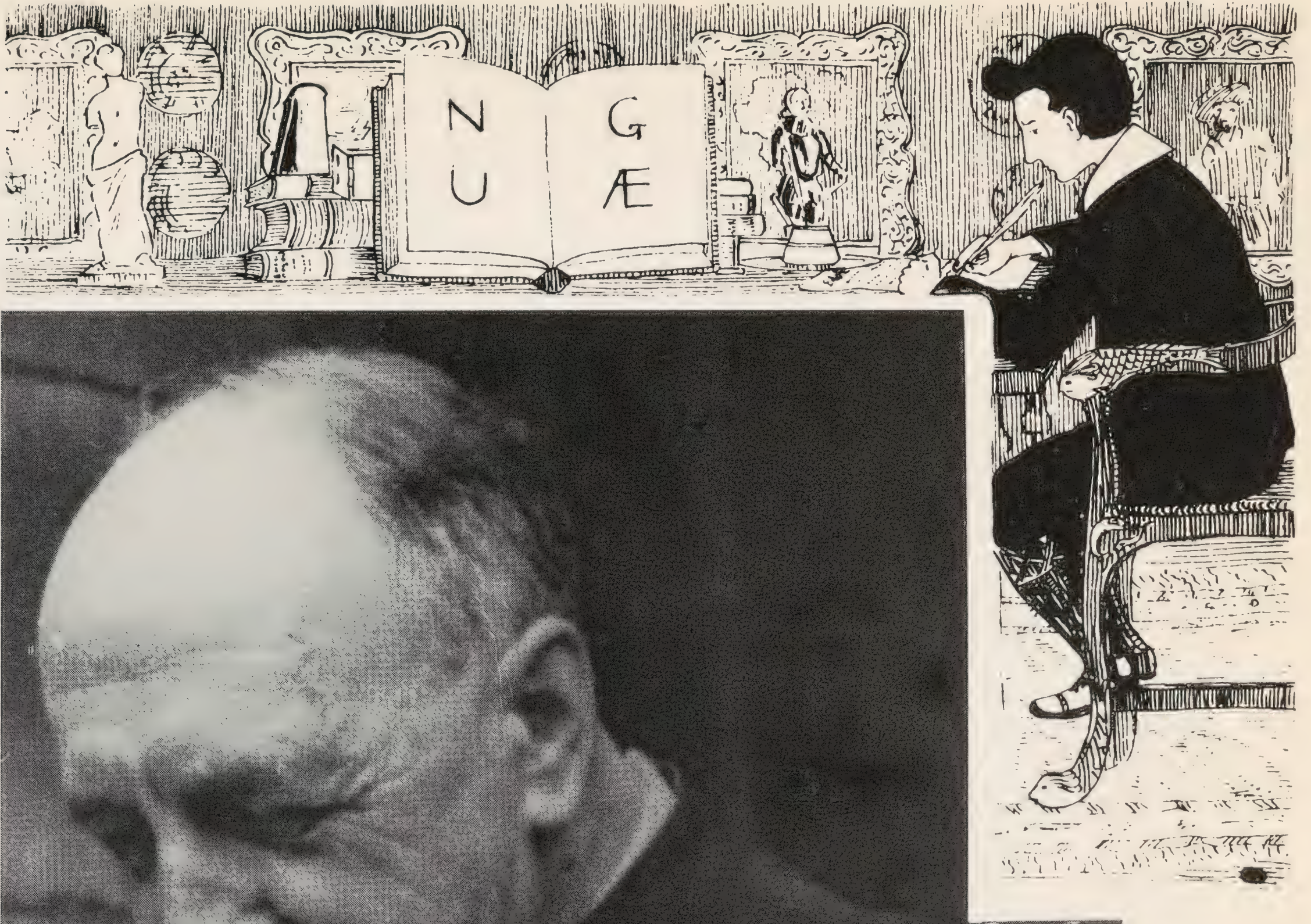
Amongst his other interesting finds was an example of *Succinea elegans* Risso, m. *scalariforme* from a pond at Polincove. The extreme difficulties under which the collection was made is indicated by the following note under *Cepaea nemoralis* (L.) "A very handsome but scarcely mature specimen of mut. *donovania* Moq. (formula 00:45) which Mr. Cribb was rearing to maturity, is preserved by him as an interesting relic of the wrecking of his quarters by an enemy bomb, the animal being killed and shell damaged by the explosion". He was then transferred to the Royal Field Artillery and was posted to Mesopotamia and Palestine where he continued collecting Mollusca. He was wounded in September 1918 and was mentioned in dispatches.

He left the Royal Field Artillery at the end of the war with the rank of Captain and in 1919 married his first wife Kathleen Dorothy Anderson, whose family came from New Zealand. Upon demobilisation he returned to his studies at Durham University where he gained his B.A. in 1920 and then entered Ripon Hall Theological College, Oxford to study for the ministry. Upon finishing his studies he was ordained by the Bishop of Coventry in 1921 and took up the appointment of curate to St. Mark's Church at Leamington Spa, Warwickshire, leaving there in 1925 to take up the post of Chaplain to the British Community in Java. Whilst in Java he continued his enthusiasm for collecting Mollusca and made substantial contributions to our knowledge of the fauna of Java, his material forming a basis for much of the monumental papers on Javanese mollusca by his close friend W. S. S. van Benthem Jutting who, at that time, was on the staff of the Zoological Museum at Buitenzorg (Bogor). W. S. S. van Benthem Jutting pays tribute to his contributions to Javanese Conchology on page 385 of her paper on Javanese pulmonate land shells, part II published in *Treubia*, thus

“of the pre-war generation mention must be made of three eminent collectors: Jonkheer W. C. van Heurn, Zoologist of the Institute of Plant Diseases and Pests; Rev. C. Th. Cribb, British parson in Java and the late Dr. E. R. Jacobson, private naturalist”. During this period in Java he spent a six month vacation in New Zealand with his wife and whilst there he again collected extensively at the same time striking up a close friendship with the eminent New Zealand conchologists Henry Suter and R. Powell. C. T. Cribb did some journalism whilst in Java being Java Correspondent of the Straits Times (a newspaper published in Singapore). Also, from 1929–1932 he was editor of Inter Ocean, a monthly magazine published in Java covering affairs in Malaysia and Australasia.

In 1932 he returned to England and was appointed Vicar of Oldbury, leaving there in 1945 to become Vicar of Moseley where he remained until his retirement in 1962. He was installed as Honorary Canon of Birmingham Cathedral in 1941. He left Birmingham to take up residence at East Sheen, London in 1962 but just before leaving the Midlands presented me with his collection of freshwater bivalves whilst his duplicate Javanese landsnails and New Zealand *Placostylus* were presented to the Natural History Department at Birmingham Museum and Art Gallery. During his period in London he visited the Society meetings. His first wife died in 1974. He is survived by his two sons, Evelyn F. T. Cribb and J. E. Rodolph Cribb and his second wife, Mrs. Kathleen (Kitty) Rodger, whom he married in 1975. His important collection of Javanese Mollusca has passed into the possession of his son Evelyn F. T. Cribb and is readily available to bona-fide research workers via the Secretary of the Conchological Society.

F. R. Woodward



C. Theodore Crabb

THE ECOLOGY OF MOLLUSCA IN ANCIENT WOODLAND. 2 ANALYSIS OF DISTRIBUTION AND EXPERIMENTS IN HAYLEY WOOD, CAMBRIDGESHIRE

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(Read before the Society, 19 November 1977)

Abstract: Analysis of distribution of molluscs in Hayley Wood shows that both abundance and diversity (number of specimens, and species, respectively, found in 30 minutes collecting) are low in the poorly drained plateau of the wood and increase on the steeper slopes of the south and west. Slope controls drainage which, in turn, affects soil pH at the surface. Poorly drained soils are more acid to a greater depth than better drained soils. Drainage is probably the main factor directly or indirectly determining mollusc distribution.

Most species tolerate coppicing: *Cepaea nemoralis* and *Deroceras reticulatum* may actually benefit from it. *Carychium tridentatum*, *Cochlodina laminata*, *Discus rotundatus* and *Euconulus fulvus* probably migrated into the Triangle (recently added adjacent woodland) from the ancient wood; *Arion hortensis* and *Oxychilus alliarius* from the old railway. *Trichia plebeia* and *Aegopinella nitidula* can move overnight at least 90 and 60 cm, respectively. They occur in densities of 4 and 1 per m² and the population of 4 m² changes every 6 and 5 days, respectively. *Cochlicopa lubrica* and *Cochlodina laminata* occur in densities of 2.5 and 0.25 per m² and their populations in 4 m² apparently change more rapidly.

This, the second of three papers on the ecology of molluscs in ancient woodland, presents an analysis of the distribution of molluscs in Hayley Wood, together with results of some experiments on the dispersal of molluscs within the wood. Basic distribution data for plants and molluscs were given in part 1 (Paul 1975).

Since the appearance of part 1 the Society's new nomenclatural lists of land and freshwater molluscs have been published (Waldén 1976, Kerney 1976). The new nomenclature is used here to maintain consistency with other recent articles in the Journal. Most changes involve the elevation of subgenera to full generic rank, but two may give rise to confusion. *Helicella caperata* (Montagu) of part 1 has become *Candidula intersecta* (Poiret) and *Retinella radiatula* (Alder) has become *Nesovitrea hammonis* (Ström). Otherwise all trivial names and specific authorities remain unchanged in the two papers.

ANALYSIS OF DISTRIBUTION

In the following analyses only records for species found alive at stations which were collected for 30 minutes by hand picking are considered. There are 60 such stations (Fig. 1), at all of which total number of species represented by live specimens (N) and total number of living specimens (n) were recorded. These two parameters are related to diversity and abundance of molluscs, respectively.

Hand picking for a fixed time is probably not as good a method of recording mollusc distribution as quadrat collecting. Both N and n are to some extent, perhaps largely, controlled by my ability to find molluscs. At stations where molluscs were rare a larger area was searched.

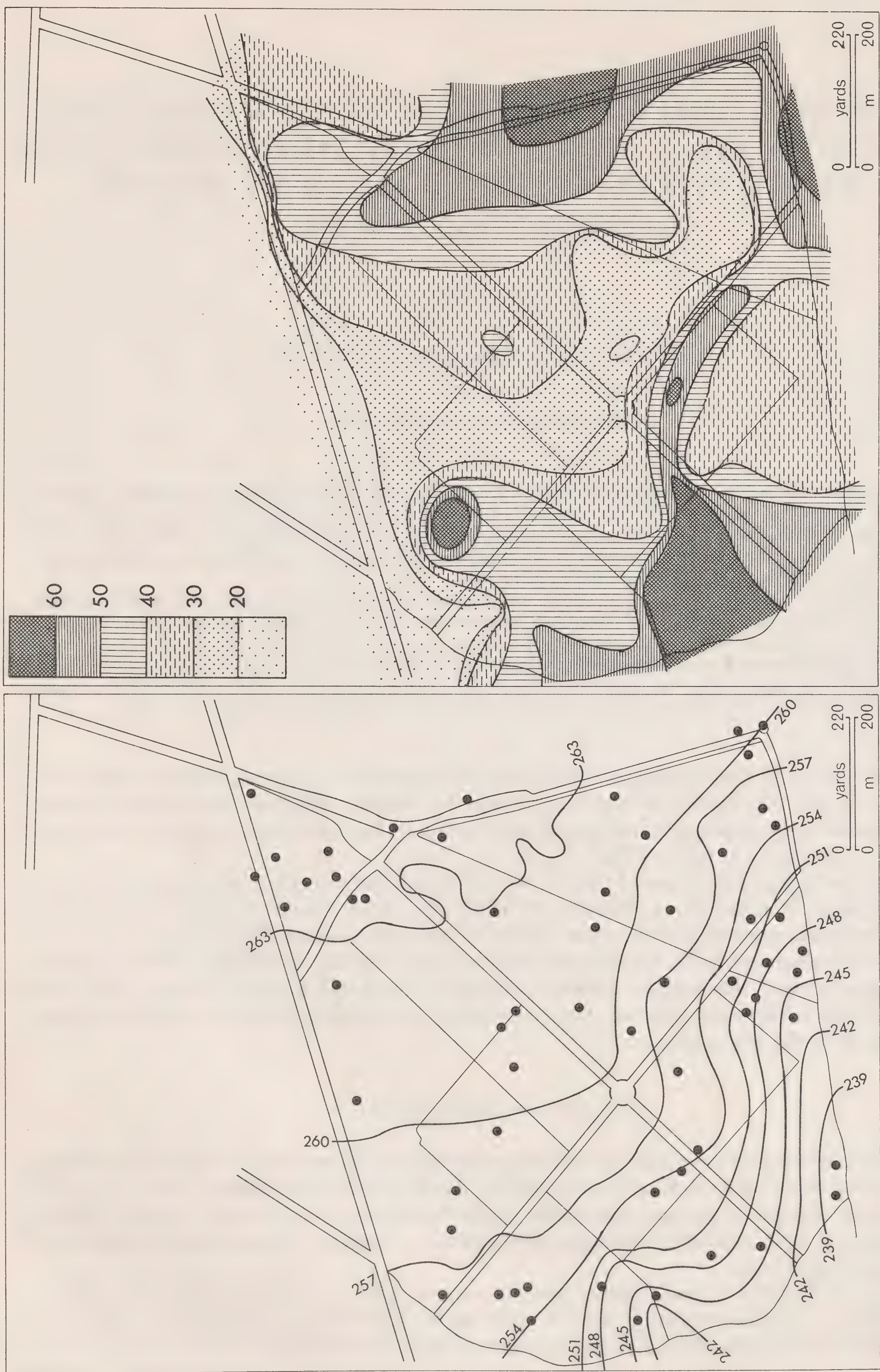


Figure 1. Contour map of Hayley Wood to show positions of 30 minute stations. Contours at 3 foot (0.91 m) intervals, redrawn after Rackham (1975, Fig. 30, p. 130).
Figure 2. Contour map of abundance of molluscs at 30 minute stations in Hayley Wood. Note that high abundance correlates well with the steeper slopes (cf Fig. 1) and vegetation zones E-G in which *Mercurialis* is abundant (Fig. 4).

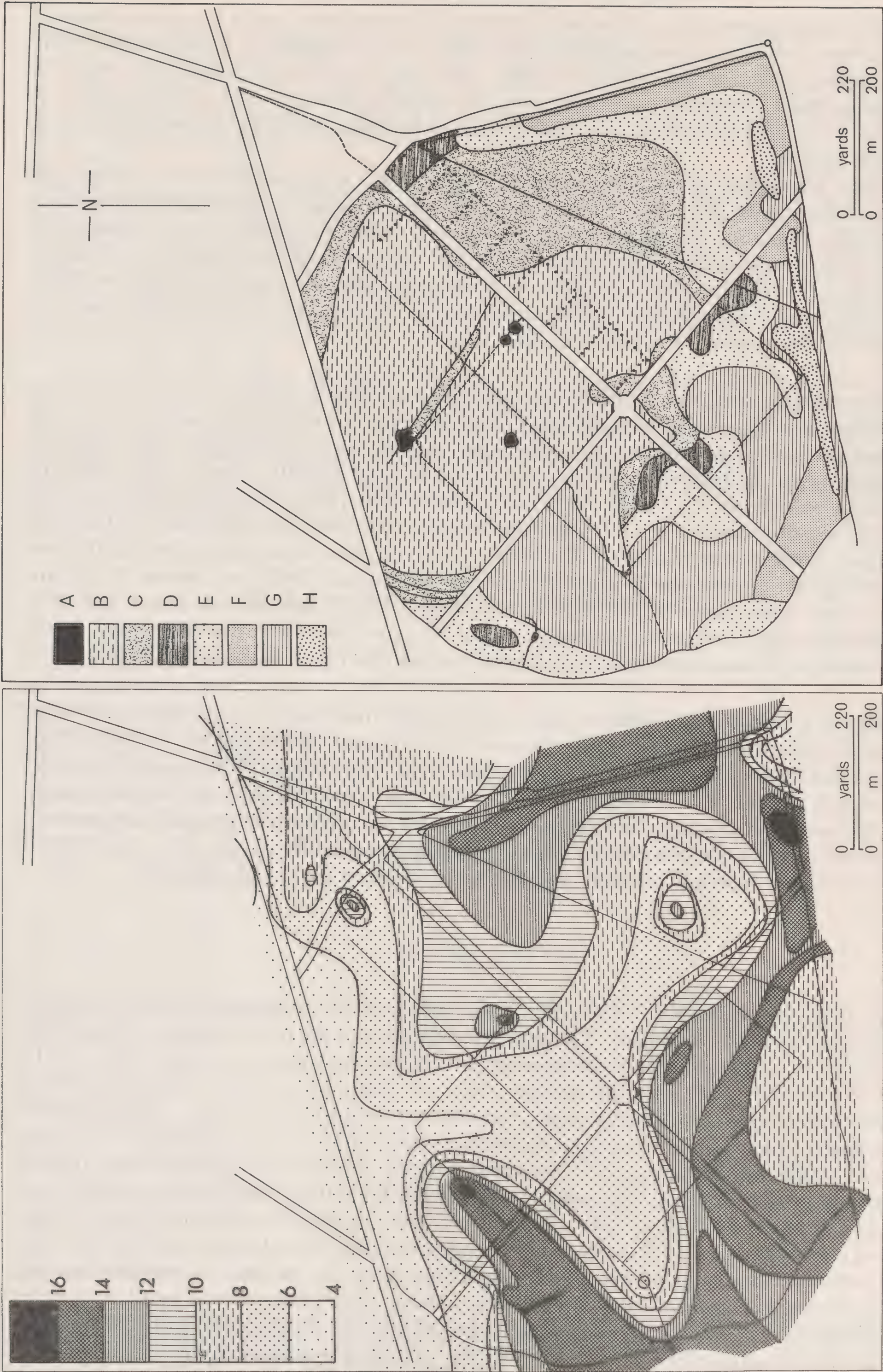


Figure 3. Contour map of diversity of molluscs at 30 minute stations in Hayley Wood. Note the broad similarity to the distribution of abundance (Fig. 2).
Figure 4. Distribution of ground vegetation zones in Hayley Wood. A. large sedge zone; B. *Primula-Filipendula*; C. *Primula-Endymion*; D. *Endymion*; E. *Endymion-Mercurialis*; F. *Mercurialis* with occasional *Endymion*; G. *Mercurialis*; H. ash swamp zone. Rackham (1975, Fig. 29, p. 123) provides a more recent and more detailed map, but the differences are only minor.

Conversely stations covered a smaller area at sites rich in molluscs. At the latter sites the time taken to record molluscs became significant. In short, the more specimens found the more time spent recording them and the less time actually collecting. Finally hand picking may overlook the smaller or more obscure species, thus giving low values for both diversity and abundance. A test of this (Paul 1975, p. 309) revealed that *Nesovitrea hammonis* was by far the most frequently overlooked species.

All three limitations of recording by hand picking for a fixed period tend to reduce the variation of the results. They should therefore tend to obscure real variation rather than reveal spurious differences. Any variation which does appear is unlikely to be due to a systematic error introduced by the collecting method. For example if abundance depended *solely* on my ability to find molluscs, N would have the same value at all stations. Diversity would also vary very little. In fact both N and n show distinct trends within Hayley Wood (Figs. 2 and 3) which correlate well with the distribution of vegetation zones (Fig. 4).

a) *Abundance*. Fig. 2. shows the distribution of n over Hayley Wood. Values of n are lowest in the coppice plots, all of which lie in zones B and C, and generally increase from zone B to zone G. Of the wettest parts of the wood, the large sedge zone (zone A) has slightly higher values than the surrounding zone B, while the ash swamp (zone H) has slightly lower values than the surrounding zones F and G. The Triangle has a median value, but the margins a low one. The mean value for all stations ($\bar{n} = 42.63$) may be used as a standard for comparison. On this basis the margins (39.0), zones A (39.50), B (36.83), C (37.16) and the coppice plots (35.0) have below average abundance; the Triangle (42.15), the ash swamp (43.83) and zone E (43.33) are about average, while zones D (45.25), F (46.50) and G (48.25) are well above average. As a broad generalization, the poorly drained parts of the wood have low abundance, the better drained parts high abundance (cf. topographic contours in Fig. 1 with pattern of Fig. 2).

b) *Diversity*. Fig. 3 shows that N has a distinct and parallel trend to n. The average value for all stations is 10.68. Mean values for stations in zone B (7.0), zone C (8.66) and the Triangle (7.66) are low; values for zone D (11.0), the coppice plots (10.75) and margins (9.5) are about average, while zones E (12.66), F (11.50) and G (12.25) are high. Zone A (12.5) and the ash swamp (12.0) also have high diversity, at least partly due to the occurrence of hygrophilous species in addition to the more typical woodland species. Although details differ, again the poorly drained parts of the wood show low diversity and the better drained parts high diversity.

EXPERIMENTS

a) *Effects of coppicing on molluscs*. Hayley Wood was coppiced for several hundred years, perhaps since before the Norman Conquest. The practice ceased about the time of the First World War when it became uneconomical and for the next half century the wood was largely neglected. Its present state is not typical. The high canopy is now very dense which reduces light and restricts low herbs. Shrubs of hazel (*Corylus avellana*), hawthorn (*Crataegus oxyacanthoides*) and blackthorn (*Prunus spinosa*), which would have been cut every 5–15 years, have run wild and are very dense in places. Fallen and rotten wood is abundant with an attendant richness in fungi. Under efficient coppicing everything was used: from fine twigs for wattle-and-daub to standard trees for structural timber (Rackham 1967). Fallen and rotten wood were virtually unknown. Any surviving native mollusc must have been able to withstand the effect of coppicing. Possibly some species may have colonized the wood since coppicing ceased. For example *Discus rotundatus* and *Cochlodina laminata* are typically found under fallen wood, while *Limax maximus* and *L. marginatus* feed on fungi. Other evidence strongly suggests that all four species are in fact truly native to the wood, nevertheless the effects of coppicing on the present day mollusc fauna are instructive.

Fortunately the practice was reintroduced experimentally in the winter of 1963/64, since when an acre a year has been cleared. In 1971 eight annual coppice plots existed.

The immediate effects of coppicing are to increase light and wind and to decrease shelter. Currently there is no market for coppice products so much wood is burnt and timber piled up. Both fire sites and log piles constitute special sites for molluscs and the latter compensate to some extent for the lack of shelter. If coppicing is completed before spring growth begins, low herbs suffer little damage and the first years's ground vegetation is almost identical to that which existed prior to coppicing. Thereafter rampant growth of light-loving herbs dominates for several years until the coppice under-storey re-establishes itself with the characteristic zonal herbs increasing under the more sheltered parts. In the experimental coppice plots in 1970/71 dewberry (*Rubus caesius*), sedges (*Carex riparia* and *C. sylvatica*), rushes (*Juncus conglomeratus* and *J. effusus*), meadowsweet (*Filipendula ulmaria*), willowherbs (*Epilobium* spp.) and thistles (*Cirsium palustre*) were prominent.

Attempts to investigate the effects of coppicing included collecting from stations in each coppice plot and collecting before and after coppicing in the 1970/71 plot. Altogether 12 stations, 3 sieve samples and one bulk sample (see Paul 1975, p. 308 for definition of these samples) were collected from coppice plots and random observations were made in 1966. The results are summarized in Tables 1 and 2 which show that most species now living in the wood survive coppicing quite well.

TABLE 1.
MOLLUSCS RECORDED FROM COPPICE PLOTS

Year of completion	1964	1965	1966	1967	1968	1969	1970	1971
Number of samples	1	1	3	1	2	1	4	2
<i>Carychium minimum</i> Müller	1	1	1	1	1	—	—	—
<i>C. tridentatum</i> (Risso)	1	d	—	—	p	—	—	—
<i>Cochlicopa lubrica</i> (Müller)	1	1	2	—	2	1	—	1
<i>Columella edentula</i> (Draparnaud)	—	—	—	—	1	—	—	—
<i>Acanthinula aculeata</i> (Müller)	—	—	—	—	—	—	—	1
<i>Punctum pygmaeum</i> (Draparnaud)	1	1	—	1	—	—	—	—
<i>Discus rotundatus</i> (Férussac)	1	—	1	1	1	—	3	2
<i>Arion ater</i> (L.)	—	1	2	—	p	—	1	1
<i>A. subfuscus</i> (Draparnaud)	—	—	—	—	—	—	1	—
<i>A. circumscriptus</i> (Johnston)	—	—	1	—	1	1	—	1
<i>A. hortensis</i> (Férussac) agg.	—	1	2	—	—	—	—	—
<i>A. intermedius</i> (Normand)	—	1	2	1	—	1	4	p
<i>Vitrina pellucida</i> (Müller)	—	—	—	—	—	—	—	d
<i>Vitrea crystallina</i> (Müller)	1	1	2	—	1	—	—	1
<i>Nesovitrea hammonis</i> (Ström)	—	d	3	—	2	1	—	2
<i>Aegopinella nitidula</i> (Draparnaud)	1	d	2	1	1	1	4	1
<i>Oxychilus cellarius</i> (Müller)	1	—	1	—	1	—	1	2
<i>O. alliarius</i> (Miller)	1	—	2	—	1	1	1	1
<i>O. helveticus</i> (Blum)	—	—	2	—	1	—	1	1
<i>Limax maximus</i> (L.)	—	1	1	—	p	—	—	—
<i>L. marginatus</i> (Müller)	—	—	—	—	—	—	1	—
<i>Deroceras reticulatum</i> (Müller)	1	—	—	—	p	1	3	1
<i>Econulus fulvus</i> (Müller)	1	1	3	1	2	—	1	1
<i>Cochlodina laminata</i> (Montagu)	—	—	1	1	1	—	2+d	p
<i>Trichia plebeia</i> (Draparnaud)	1	1	2	1	1	1	3	1
<i>Cepaea nemoralis</i> (L.)	1	—	1	—	1	1	1+d	p
TOTAL SPECIES*	13	13	18	7	19	9	14	17

* Assumes species represented by dead shells only actually live in the coppice plots. Numbers indicate the number of samples from each coppice plot in which a species was found, p. indicates a random observation, d dead shells only. The 1971 figures do not include pre-coppicing samples.

TABLE 2.
SPECIES RECORDED BEFORE AND AFTER COPPICING IN THE 1970/71 PLOT

Species	Before			After		
	R.O.	B.S.	St. 24	R.O.	S.S.	St. 24a
<i>Cochlicopa lubrica</i> (Müller)	—	2	1	—	—	4
<i>Acanthinula aculeata</i> (Müller)	—	—	—	—	1	—
<i>Discus rotundatus</i> (Férussac)	1	3	4	p	2	9
<i>Arion ater</i> (L.)	—	—	—	p	—	1
<i>A. circumscriptus</i> (Johnston)	1	—	—	p	—	6
<i>A. intermedius</i> (Normand)	3	—	1	p	—	—
<i>Vitrina pellucida</i> (Müller)	—	—	—	—	—	1d*
<i>Vitrea crystallina</i> (Müller)	—	3	—	—	—	1
<i>Nesovitrea hammonis</i> (Ström)	—	1	—	—	2	1
<i>Aegopinella nitidula</i> (Draparnaud)	4	3	35	p	—	9
<i>Oxychilus cellarius</i> (Müller)	—	—	—	p	1	1
<i>O. alliarius</i> (Miller)	—	1	—	p	—	1
<i>O. helveticus</i> (Blum)	—	—	—	p	—	1
<i>O. sp.</i> (juvenile)	3	—	1	—	—	—
<i>Deroceras reticulatum</i> (Müller)	—	—	—	p	—	1
<i>Euconulus fulvus</i> (Müller)	—	1	—	—	—	1
<i>Cochlodina laminata</i> (Montagu)	1	1	1	p	—	—
<i>Trichia plebeia</i> (Draparnaud)	1	—	7	p	—	5
<i>Cepaea sp.</i> (? <i>nemoralis</i>)	—	—	—	p	—	—
TOTAL SPECIES	7	8	7	12	4	13 (+1d)
	11 (+1)			17 (+1)		
TOTAL SPECIMENS			50			41

R.O. random observation; B.S. bulk sample; St. Station; S.S. sieve sample.

* Station 24a was collected 25 May 1971, which is too late in the year for live adult *V. pellucida* and very early for live juveniles. There is no reason to suppose that *V. pellucida* was not still living in the 1970/71 coppice plot. Numbers indicate the number of living specimens of each species. Note the increase in diversity after coppicing, although there is a slight decline in abundance between stations 24 and 24a. The data do not indicate strongly adverse affects of coppicing.

b) *Migration of molluscs into the Triangle.* The Triangle is an area of modern woodland adjacent to the ancient wood. Typical woodland molluscs might be expected to migrate into the Triangle from the ancient wood as soon as the former became a suitable habitat. Migration from other sources such as the ditches and hedges bounding the Triangle cannot be neglected however.

Information on the rate at which molluscs colonize a new suitable habitat is essential in trying to distinguish any native molluscs in the wood from more recent introductions. If a newly introduced species can spread through the entire wood in a year or two, there is little chance of detecting its introduction other than by the chance of collecting at the exact time of introduction. If the rate of colonization is much slower then there is a correspondingly greater chance of detection. With this idea in mind eight stations and five sieve samples were collected in the Triangle to try to detect which molluscs were present and whence they originated. The sieve samples were taken at approximately 20 m intervals on a line running directly away from the north section of the ancient wood up to the old railway. The stations are more randomly distributed. Table 3 lists the occurrence of species in the Triangle.

c) *Dispersal rates of Aegopinella nitidula and Trichia plebeia.* These two species are the most abundant and widespread in the main wood and were used for experiments to detect how far they could travel overnight and how widely they might disperse. Two experiments were run commencing on 22 April and 12 May, 1971. The first was deemed unsatisfactory as less than half the original specimens released yielded data, some died, the others were just not recaptured

TABLE 3.
DISTRIBUTION OF MOLLUSCS IN THE TRIANGLE

SPECIES	SAMPLE ¹												
	Q	25	R	16	77	35	S	78	T	U	34	33	66
<i>Carychium minimum</i> (Müller)	—	—	—	—	—	—	1	—	—	—	—	—	—
<i>C. tridentatum</i> (Risso)*	1	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cochlicopa lubrica</i> (Müller)	5	1	2	—	2	1	2	—	6	5	—	—	6
<i>Acanthinula aculeata</i> (Müller)	4	—	2	—	—	—	—	—	—	1	—	—	—
<i>Punctum pygmaeum</i> (Draparnard)	—	—	1	3	—	—	1	—	7	—	—	—	—
<i>Discus rotundatus</i> (Férussac)*	3	1	—	1	2	5	—	4	—	—	—	—	—
<i>Arion circumscriptus</i> (Johnston)	—	2	—	—	3	—	—	1	—	—	3	1	—
<i>A. hortensis</i> Férussac agg.†	—	—	—	—	—	—	—	—	—	—	—	—	2
<i>Vitrina pellucida</i> (Müller)	—	—	—	—	—	1	—	—	—	2	—	—	d
<i>Vitrea crystallina</i> (Müller)	2	—	—	d	2	—	—	2	1	—	—	—	3
<i>Nesovitrea hammonis</i> (Ström)	2	—	—	—	—	—	—	—	3	1	—	—	3
<i>Aegopinella nitidula</i> (Draparnaud)	1	22	—	1	17	21	1	17	8	1	23	10	3
<i>Oxychilus cellarius</i> (Müller)	—	—	—	—	1	2	—	—	—	—	2	—	—
<i>O. alliarius</i> (Miller)†	—	—	—	—	—	—	1	2	3	1	2	1	2
<i>O. helveticus</i> (Blum)	—	—	—	—	3	6	—	3	—	—	—	—	—
<i>Deroceras laeve</i> (Müller)	—	—	—	2	—	—	—	—	—	—	—	1	—
<i>Euconulus fulvus</i> (Müller)*	—	—	1	—	—	—	—	—	—	—	—	—	—
<i>Cochlodina laminata</i> (Montagu)*	1	1	—	—	1	—	—	—	—	—	—	—	—
<i>Trichia plebeia</i> (Draparnaud)	—	12	—	—	2	4	1	1	1	—	2	2	—
<i>Cepaea nemoralis</i> (L.)	—	—	—	—	—	d	—	—	—	—	—	—	—
D1	25	30	48	50	53	60	65	68	82	100	108	135	195
D2	62	92	48	150	53	92	35	12	22	10	20	12	10
D3	117	85	117	5	107	57	117	150	115	115	92	90	17

D1 = distance from ancient wood (in m.); D2 distance from old railway; D3 distance from Hayley Lane.
* Species which probably migrated in from the ancient wood. † Species which probably migrated from the railway.
¹ Numbers refer to stations, letters to sieve samples.

TABLE 4.
DISPERSAL OF *TRICHIA PLEBEIA* AND *AEGOPINELLA NITIDULA*

SPECIES AND TIME	DISTANCE (CM)									
	20	40	60	80	100	120	140	160	180	TOTAL
<i>T. PLEBEIA</i> (32)										
1. 12 hours 10 minutes	10	4	6	4	1	—	—	—	—	25
2. 23 hours 30 minutes	8	9	5	5	—	—	—	—	—	27
3. 47 hours 30 minutes	2	8	1	2	2	3	—	—	—	18
4. 108 hours 30 minutes	1	2	3	2	2	3	—	3	3	19
<i>A. NITIDULA</i> (36)										
1. 12 hours 10 minutes	9	13	3	1	—	—	—	—	—	26
2. 23 hours 30 minutes	12	10	4	1	—	—	—	—	—	27
3. 47 hours 30 minutes	10	11	6	0	1	—	—	—	—	28
4. 108 hours 30 minutes	1	1	5	5	6	1	—	—	—	19

during the first search. The second experiment involved freshly collected snails together with a small number carefully kept in captivity for three days. They were released in a vegetation-free area of the south section at 20:00 hours. Results are shown in Table 4 which reveals an overall migration away from the release point, although 108.5 hours after release two living snails remained within 20 cm of the release point. During the final experiment (next section) four living *Trichia* were found within 175 cm of the release point 69½ days after release, the closest only 76 cm from the release point.

12½ hours after release 25 of 32 *T. plebeia* and 26 of 36 *A. nitidula* were relocated, the furthest 89 cm (*T. plebeia*) and 60 cm (*A. nitidula*) from the release point. Assuming the snails move

randomly, these recorded maxima could represent individuals which moved in more or less straight paths away from the release point. However, even these snails could have followed tortuous paths to their resting sites. Thus it can be concluded that *T. plebeia* can move at least 89 cm overnight and *A. nitidula* at least 60 cm.

The conditions of both experiments were artificial in that a very high density of snails was created at the outset. Perhaps they were stimulated to move further than normal by overcrowding or to remain together and mate. This led to the final experiment on turnover rate for a given area of the wood.

d) *Rate of turnover of mollusc populations.* This experiment was conducted in the same clearing as the second dispersal experiment. A 2 m by 2 m square was divided into four 1 m squares. All snails within all four squares were marked, their positions recorded and they were replaced exactly where found. The squares were searched daily in sequence, starting with a different square each day, for a further ten days. New snails were marked and replaced and the positions of all snails recorded every day. Unfortunately, the 11 day period (20 to 30 July, 1971 inclusive) coincided with a dry spell and mollusc movement may have been less than normal. Only the four most common species, *Cochlodina laminata*, *Aegopinella nitidula*, *Trichia plebeia* and *Cochlicopa lubrica*, were involved. Results are given in Table 5.

TABLE 5.
RESULTS OF TURNOVER EXPERIMENT

	<i>C. lubrica</i>	<i>A. nitidula</i>	<i>C. laminata</i>	<i>T. plebeia</i>
Average number present	10.5	3.8	1.2	17.7
net loss/gain*	+11 (-3d)	-2 (-1d)	-1	-11 (-10d)
average new arrivals	3.3/day	0.7/day	0.5/day	2.6/day
average departures	1.9/day	0.9/day	0.6/day	3.7/day
average mortality	0.3/day	0.1/day	—	1.0/day
mean turnover	2.6/day	0.8/day	0.55/day	3.015/day
% turnover	25%	21.5%	45%	17%
approximate number of days for complete turnover	4	5	2	6

* Figures here ignore the number of dead (given in parentheses).

The figure of 10 dead for *T. plebeia* is lower than quoted in the text because four specimens were found dead on the first day and removed before the experiment began. A further three were found on the last day just outside the area of the experiment and are hence not included in the table.

During the period of the experiment the populations of *A. nitidula*, *Cochlodina laminata* and *T. plebeia* declined, while that of *Cochlicopa lubrica* apparently increased. Ignoring mortality for the moment, these trends were probably temporary and neither rate of introduction nor rate of departure can be accepted as the better measure of the rate of turnover. In Table 5, mean turnover rate is the average of the rates of introduction and departure. Percentage mean turnover is the rate of turnover expressed as a percentage of the mean population of 4 m². From this it can be seen that, on average, the populations of these four species in a 4 m² area apparently change every two to six days.

DISCUSSION

a) *Distribution.* The appearance of Rackham's book on Hayley Wood (Rackham 1975) has provided a wealth of information not available when part 1 was prepared. Some of this information goes a long way towards explaining the distribution of molluscs within the wood. In chapter 3 (Rackham 1975, pp. 121-132) convincing evidence is presented that drainage is the

principal factor controlling the distribution of ground vegetation zones (Fig. 4). *Mercurialis perennis* cannot withstand water-logging, particularly during spring growth, because the gleyed boulder clay soil releases ferrous iron. In laboratory experiments *Mercurialis* succumbed to water culture with 2–4 parts per million (ppm) Fe^{2+} , *Endymion nonscriptus* to 5–10 ppm and *Primula elatior* to 20–30 ppm. *Mercurialis* forms carpets and grows most successfully on the steeper, better drained slopes of the south and west (cf. Figs. 1 and 4). *Primula elatior* is shaded out by *Mercurialis* with which it cannot compete, although it will grow very well on the better drained slopes if *Mercurialis* is removed. Thus *Primula* dominates on the poorly drained plateau where *Mercurialis* cannot survive because of the waterlogging of the soil. *Endymion* does not grow well in badly waterlogged parts of the wood, but is more tolerant than *Mercurialis*. Although mature *Endymion* can compete with *Mercurialis* the juvenile plants are shaded out just as *Primula elatior* is. Thus a combination of drainage characteristics and competition between the principal ground herbs controls the distribution of the ground vegetation zones.

Waterlogging of the boulder clay soils not only releases iron, but affects soil pH directly or indirectly. Martin and Piggott (in Rackham 1975, p. 64) present four soil profiles to depths of 65 cm in zones B, C, F and G which show that poorly drained soils are more acid to a greater depth than better drained soils. An associated factor is that calcium carbonate was not detected until depths of 65 cm (zone B), 47 cm (zone C), 30–40 cm (zone F) and 5–10 cm (zone G), respectively. Soil acidity in this case results from depth of leaching by surface waters. On the basis of 40 measurements all taken at 15 cm depth, Rackham (1975, p. 69) found a highly significant correlation ($p < 0.001$) between mean pH and vegetation zone.

Clearly, although Hayley Wood lies on chalky boulder clay which contains pebbles and boulders of chalk and other limestones and has abundant free calcium carbonate, drainage has markedly altered the pH of surface soil over most of the wood. Comparisons with mollusc distributions in woods investigated by Berry (1973) and Wäreborn (1969, 1970) may be valid, despite the more acid or calcium carbonate-free substrates of these woods and the different methods of sampling employed. Where calcium carbonate is not available directly in soils, calcium and other bases are extracted from the substrate by trees and accumulate in the leaves usually as salts of organic acids. These in turn are added to the leaf litter and förna where the calcium may become available to molluscs. Wäreborn maintains that calcium oxalate, which occurs in leaves of oak and beech, is less readily available to molluscs and has 'no (or almost no) effect on pH', whereas 'In leaves of ash and probably also lime, maple and elm, most calcium salts are easily dissolved and decidedly alkaline, e.g. calcium citrate' (Wäreborn 1969, p. 465). A similar process must occur in Hayley Wood and quite possibly litter and förna form the principal source of calcium for molluscs in the more acid, poorly drained parts of the wood. Apart from the general dependence of molluscs on high humidity, availability of moisture also has an indirect effect on the availability of calcium by speeding up the decomposition of litter and Berry (1973, p. 35) concluded that 'subdued activity in leaf litter is a good general indication of paucity of snails, both in terms of numbers and species.' This again is true of Hayley Wood where accumulations of undecayed dead leaves produce very few or no molluscs (Paul 1975, p. 326).

Wäreborn (1969, 1970) investigated five types of woodland, moist oligotrophic mixed woods, drier mixed woods, oak woods, and moist and drier 'meadow woods'. The latter two had the most abundant and diverse mollusc faunas and are probably the most comparable to Hayley Wood. In the moist mixed woods and oak woods Wäreborn found a strong correlation ($p < 0.05$) between abundance of molluscs and calcium content of the förna (1969, fig. 7, p. 469; fig. 8, p. 471), but no significant correlation was found in other types of wood. In the drier meadow woods a highly significant correlation ($p < 0.01$) occurred between moisture content and abundance (1969 fig. 9, p. 476). Moist meadow woods had the most abundant fauna, highest pH values and highest calcium content of förna. Although no calcium analyses of förna are available for Hayley Wood, it seems quite plausible that the same factors affect abundance of

molluscs. Abundance is highest on the better drained slopes of the south and west where *Mercurialis* predominates, ash trees are very common and pH is high. Presumably calcium is abundant and available, moisture is high and relative humidity is kept high by the mercury carpet. Abundance is lowest on the plateau where oaks are more common (although ash trees still occur) ground herbs are sparse and pH is lower. Furthermore the ground dries out in dry summers.

As regards relative humidity (RH) the distributions of *Nesovitrea* and *Aegopinella* spp. may be significant. Morden (1977, p. 63) found the following in desiccation experiments at 90%RH: *Nesovitrea hammonis* survived for 132 days, *Aegopinella nitidula* for 71 days and *A. pura* for 24 days. In Hayley Wood *N. hammonis* is commonest in zones B, C and H (ash swamp); *A. nitidula* is abundant everywhere, while *A. pura* has a predominantly southern and western distribution in zones E, F and G (Paul 1975, fig. 8). Although zones B, C and H are the wettest parts of the wood in winter, they dry out considerably in dry summers and thereby may become unsuitable habitats for the drought-sensitive *A. pura*. Unfortunately this evidence is not conclusive since *N. hammonis* is apparently the most acid tolerant as well as the most drought resistant of the three species. It would be useful to know the pH and desiccation tolerances of other molluscs living in Hayley Wood.

Diversity and abundance have similar relationships to environment. Wäreborn (1970, fig. 2, p. 287) found a significant correlation between diversity and calcium content of förna only in the drier mixed woods. pH shows a distinct trend with diversity, but no statistics are quoted. Berry (1973) found the most diverse faunas in Ham Street Wood occurred in valleys, where moisture and nutrients were highest and presumably litter decay fastest. Again, in Hayley Wood diversity correlates well with drainage and ground vegetation, being high on the mercury slopes and low on the plateau. The unexpectedly high values for zones A (large sedge) and H (ash swamp) are at least partly due to the occurrence of hygrophilous species, e.g. *Columella edentula*, which are virtually confined to these two zones.

In conclusion it would seem that the drainage behaviour of Hayley Wood controls the distribution of plants and molluscs, directly by waterlogging which makes parts of the wood unsuitable for certain species; and indirectly by affecting pH and availability of calcium in litter and förna. If this is so the similar patterns of distribution for molluscs (Figs. 2 and 3) and ground vegetation zones (Fig. 4) are not so surprising, although it would seem an unwarranted assumption that plant distribution directly controls mollusc distribution. Any effect plants have is probably indirect through their contribution to litter and förna.

b) *Effects of coppicing.* Berry (1973, p. 35) concluded that coppicing was deleterious to molluscs in Ham Street Wood, 'Cutting and the associated disturbance of the substrate eliminate Mollusca almost completely', although he qualified this later. 'Prior to cutting, dense coppice stands of a single tree species are, in any event, host to few snails and it may be that not much is lost.' (Berry 1973, p. 35). Experience in Hayley Wood suggests that the latter is more likely and that the apparent absence of molluscs after coppicing in Ham Street Wood may be due mainly to their initial low concentrations. In Hayley wood most species survive coppicing quite well. 16 species are known from Hayley Wood in addition to those listed in Table 1 from the coppice plots (Paul 1975, table 3, p. 310, and p. 311). Of these, four are freshwater species and a fifth, *Deroceras laeve*, is a strongly hygrophilous slug; three are each known from a single dead shell; and a further five are marginal species not found within the main body of the wood. There is no reason at all to expect to find any of these within the area of the coppice plots in Hayley Wood. Of the remaining three species, *Azeca goodalli* is extremely local and not known to live anywhere near the coppice plots, while *Aegopinella pura* and *Cepaea hortensis* have predominantly southern and western distributions (Paul 1975) and are known from a ditch site between the coppice plots and the adjacent main ride. Both could simply have been overlooked, or their absence need have nothing to do with coppicing. There is thus no single species which one might expect to find in

the coppice plots which is, in fact, absent.

Arion subfuscus, *Vittrina pellucida*, *Limax marginatus* and *Acanthinula aculeata* are rather rare, but again have southern and western distributions so their scarcity may also be original. *Euconulus fulvus* is better represented than I would normally expect, but this may reflect its habit of hiding under bark on fallen logs which are abundant in the coppice plots. *Deroceras reticulatum* shows an apparent increase after coppicing which could reflect decreased shelter concentrating the slugs and making them easier to find. Alternatively populations of this 'field slug' may increase in response to the increase in phototropic herbs particularly since Pallant (1969) found a significant correlation between *D. reticulatum* and ground herbs in woodland. Similarly, live records of *Cepaea nemoralis* are more common in the coppice plots than elsewhere, perhaps reflecting the increase in shelter from predators afforded by the rampant vegetation.

Cochlodina laminata, *Discus rotundatus* and *Limax maximus* all survive coppicing. They are unlikely to be recent introductions, especially since the latter is totally absent from the Triangle and the former pair have only migrated into part of it. If they have not colonized this small area since 1922, they are unlikely to have colonized the entire wood since 1914. All three species are typically found under logs and dead wood. Presumably under coppicing as formerly practised they would have lived on the coppice 'stools' and around the bases of standard trees.

Table 2 shows that more species were found alive after, than before, coppicing in the 1970/71 plot, although a slight decrease in the number of specimens found in 30 minutes occurred. To summarize, the majority of species apparently withstand coppicing. A few may actually benefit and those species which respond unfavourably are likely to have survived since by no means all the wood was coppiced in any one year. There are no clear indications that coppicing is seriously injurious to any mollusc species. Since coppicing, even as formerly practised, undoubtedly diversifies the habitats available to molluscs within the wood, it is not surprising that one or two species seem to benefit from the practice.

c) *Migration*. Information on the actual or potential rate of movement of molluscs into new environments or within existing habitats is scanty and it is certainly not possible yet to characterize most species as 'adventurous', 'migratory', 'static', etc. With regards to migration into new environments, a few species seem to have colonized the Triangle very slowly and their sources can be suggested. *Carychium tridentatum*, *Discus rotundatus*, *Euconulus fulvus* and *Cochlodina laminata* probably migrated in from the ancient wood, whereas *Arion hortensis* and *Oxychilus alliarius* almost certainly migrated in from the old railway. Other species are either too widely dispersed or too rare to be certain of their original source. Rate of colonization of the Triangle is not related to the size of the species involved, even though foot length is broadly related to the distance a gastropod can travel in a given time (e.g. overnight). In this case suitability of the environment is the most probable factor controlling migration. This is suggested by the following facts:—

1. The largest (foot length) species (*Arion ater*, *Limax maximus*) are absent, which may reflect the lack of suitable shelter for these slugs and also the tendency of the Triangle to dry out in summer due to the sparse ground vegetation.

2. *Deroceras laeve*, a particularly hygrophilous slug, is confined to two sites very close to, or actually in, marginal ditches or pools.

3. *Punctum pygmaeum*, the smallest species, although rare occurs at least 50 m away from any possible source and the center of the Triangle is only 75 m from these sources. However, passive dispersal is quite likely to effect minute snails like *Punctum*.

4. *Discus rotundatus* and *Cochlodina laminata*, both normally found on fallen logs, clearly migrated in from the ancient wood. Neither has penetrated much further than the ground vegetation of the ancient wood; *C. laminata* 55 m and *D. rotundatus* 68 m. The ground vegetation had reached about 50 m in 1970/71.

As to movement within a suitable habitat, Humphreys (1976, p. 102) marked and released

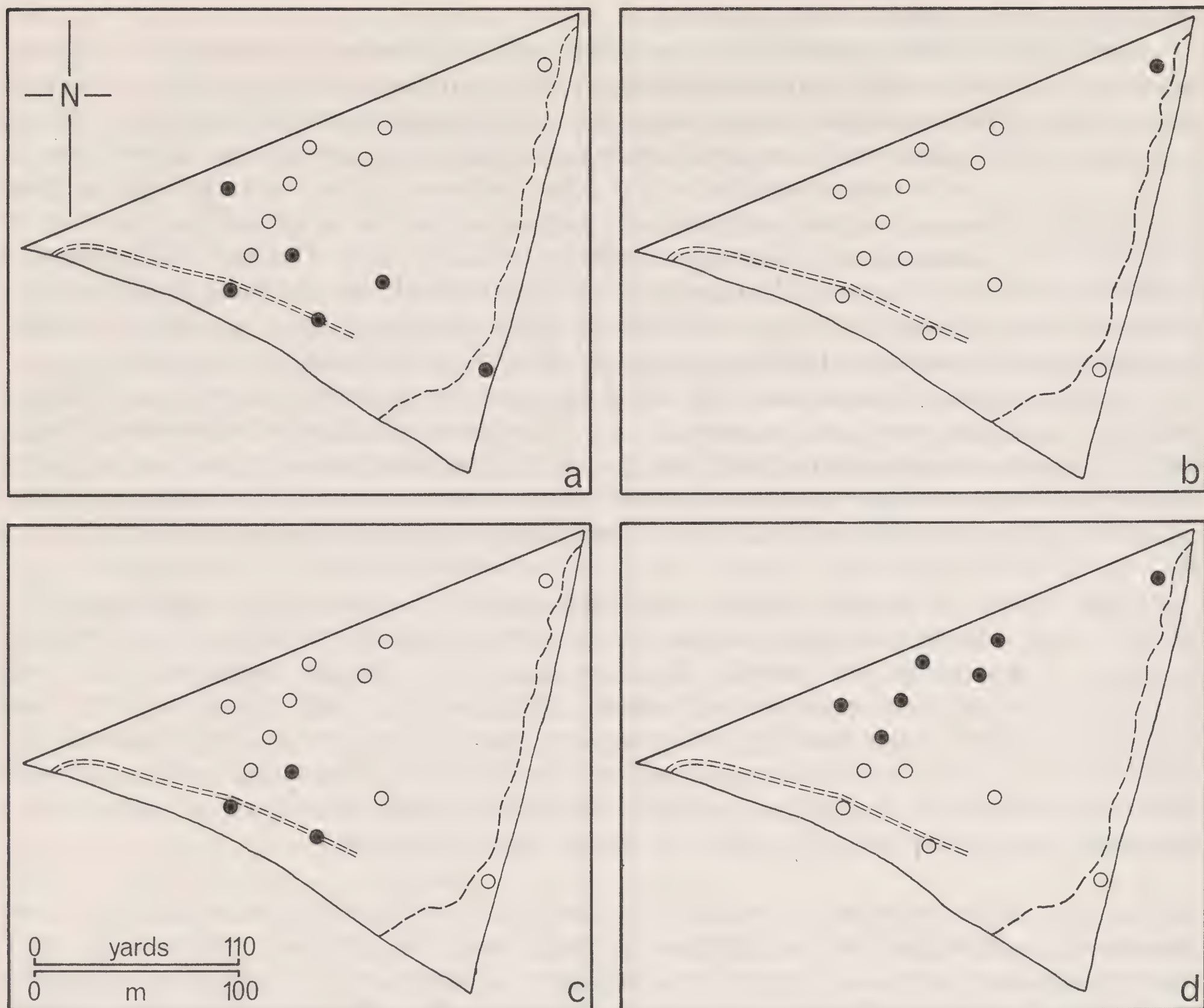


Figure 5. Occurrence of a) *Discus rotundatus*, b) *Arion hortensis* agg., c) *Cochlodina laminata* and d) *Oxychilus alliarius* in the Triangle. Solid circles indicate presence, open circles absence. Note that a and c seem to have migrated in from the ancient wood, while b probably came from the old cottage garden across the railway, and d from the railway embankments.

10 specimens of *Theba pisana* at The Island, St. Ives, Cornwall. One specimen had moved 12 m when last seen four months after release, having remained within 1 m of the original position for the first three months. The other nine specimens remained within 1 m of their original positions for up to eight months after marking. My own experiments add a little further information about other species. Although the dispersal experiments show that *A. nitidula* and *T. plebeia* can move at least 60 and 90 cm overnight, respectively, the turnover experiments do not confirm that these species habitually move this distance. Indeed the presence of four *T. plebeia* within 175 cm of the original release point 69.5 days after release shows that at least some specimens of *Trichia* are as static as *Theba pisana* in Cornwall. The rate of turnover is very high for *Cochlodina laminata* which is present in such small numbers as to make these results suspect. Also one specimen remained just on the edge of one square and hence with relatively little movement was recorded inside and outside the square during the course of the experiment. Equally the turnover value for *Cochlicopa lubrica* is probably too high and is influenced by the apparently high rate of introduction. I believe this represents specimens which emerged from within the soil rather than ones which crawled into the area of the experiment, although this is very difficult to prove. Once marked, they become more conspicuous and I knew approximately where to look for them.

Interesting and unexpected results of the turnover experiments include the discovery of four *Trichia* 76, 84, 110 and 175 cm from the original release point of the second dispersal experiment 69.5 days after release. No marked *A. nitidula* were found, but the paint did not stick so well to their shells and their habit of burying themselves may have helped to remove it. Secondly, during the experiment 21 snails died to my knowledge; one *A. nitidula*, three *C. lubrica* and seventeen *T. plebeia*. Fifteen of the latter were crushed, but apparently not completely eaten. At first I thought I had damaged them in setting up the experiment since to mark out the squares I had to walk over the area. Thereafter searching was always done from the perimeter, taking special care not to crush specimens. Soon the discovery of crushed marked individuals made it clear that something else was killing the snails. On 29 July, 1971, I found one crushed individual on the upper surface of a leaf of *Circaea lutetiana* 14 cm above the ground. Predation by birds or squirrels seems most probably the cause, however whatever was killing them was not eating the flesh at all efficiently. More than half remained in most cases. Finally it might seem that the recorded rate of decline of *T. plebeia* (29 specimens on 20 July; 13 on 30 July) that it would become locally extinct very soon. At least one specimen is known to have deposited eggs during the course of the experiment which may well have coincided with a period of normal high mortality in the life cycle of *T. plebeia*.

CONCLUDING REMARKS

Although the available evidence is limited and much more work could be done, some conclusions about the ecology of molluscs in Hayley Wood may have more general validity. Firstly the distributions of individual species (Paul 1975), abundance and diversity are not random and show distinct trends. Molluscs are more abundant and the fauna more diverse in the better drained parts of the wood where the least acid soils occur and the almost perennial carpet of *Mercurialis* maintains nearly constant conditions of high humidity. One might expect to find more species of snails in 30 minutes where the density of snails is high and fewer species in areas of low density, thus giving an artificial impression of increased diversity. This is probably not the case in Hayley Wood since several species, e.g. *Acanthinula aculeata*, *Arion subfuscus*, *Vitrea pellucida*, *Aegopinella pura*, *Oxychilus cellarius* and *Cochlodina laminata*, are strongly associated with the better drained parts of the wood in the south and west (Paul 1975). Thus these patterns of distribution probably reflect the suitability of the habitat, although precise details remain to be determined.

This general conclusion tends to be confirmed by the rates of migration into the Triangle. Catholic species like *Aegopinella nitidula*, for which the Triangle is a suitable habitat, are widespread and presumably colonized it rapidly. The more typically woodland species *Discus rotundatus* and *Cochlodina laminata* had migrated only 68 and 55 m respectively. These snails are associated with fallen and rotten wood and *C. laminata* feeds on fungi. The Triangle largely lacks these features since all the trees are young and it may not yet have become a suitable habitat for these snails. The fact that the ground vegetation of the ancient wood has spread into the Triangle approximately the same distance may also be significant. Thus, although on average *D. rotundatus* and *C. laminata* have spread at a rate of 1.3 and 1.0 m per year, respectively, these rates may not represent their general movement within more suitable habitats. Although suspect, the relatively rapid turnover rate of *C. laminata* tends to support this conclusion.

As to general rates of migration, *T. plebeia* and *A. nitidula* may move at least 90 and 60 cm overnight, respectively. If maintained continuously throughout the year, this would result in 330 and 220 m of travel. The longest diagonal of Hayley Wood is approximately 1 km. It is therefore possible in theory, although highly unlikely in practice, that these two species could colonize the entire wood from a remote corner in three to five years by their own unaided efforts. When other means of passive dispersal are taken into account, these potential rates of migration

may not be so unreasonable. All the species living within the ancient wood have probably had ample time to occupy all available habitats which makes the occurrence of some very local species puzzling. *Azeca goodalli* is characteristically local in Britain, but *Clausilia bidentata* is not and its absence over most of Hayley Wood is very unexpected.

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THE ECOLOGY OF MOLLUSCA IN ANCIENT WOODLAND. 3 FREQUENCY OF OCCURRENCE IN WEST CAMBRIDGESHIRE WOODS

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(Read before the Society, 19 November 1977)

Abstract: Ancient woods in the west Cambridgeshire area fall into three categories: 1. those which retain their management structure and a rich flora, 2. Forestry Commission plantations recently cleared and replanted with conifers and 3. elm dominated woods with a thick ground flora of grasses. Mollusc fauna is richest in woods of the first group and poorest in those of group three, but the fauna of the recent plantations will decline seriously soon. Modern woodland is distinguished as adjacent to, or isolated from, ancient woodland.

Ancient woodland mollusc fauna falls into four groups: 1. freshwater species found in streams and pools, 2. almost ubiquitous species found in a wide variety of habitats, 3. common species generally restricted to woodland in East Anglia but more widely dispersed elsewhere in Britain and 4. relatively rare species which in East Anglia are confined to woodland. The original Atlantic mollusc fauna is likely to have been composed of elements from all four groups. Modern woodland adjacent to ancient has a richer mollusc fauna than isolated modern woods since some ancient woodland species colonize new areas of woodland relatively rapidly. Even so, only species of group four are conspicuously absent from isolated modern woods.

This, the last of three papers, lists the occurrence of molluscs in all the woodlands visited during the study (Fig. 1). Brief descriptions of the types of woodland are presented, together with some comments on the relative abundance of species of molluscs. Most woods, other than Hayley Wood, were only visited 1-5 times, so the lists of molluscs are not definitive, but they do give a general idea of relative abundance. Using evidence presented by Rackham (1967, 1975 and personal communications), I have accepted a number of woods in west Cambridgeshire and adjacent areas as ancient, i.e. at least part of these woods has probably been woodland continuously since postglacial afforestation. For comparative purposes I also collected in two patches of more recent woodland which are completely separated from ancient woods (Fig. 1). Further information was gathered by collecting in the modern parts of Hayley and Madingley woods, for which detailed historical data were made available by Oliver Rackham. Probably all the other ancient woods contain some modern additions (certainly the southern part of Potton Wood was ploughed extensively in Medieval times and parts of Eversden Wood have been added since the 1891 Ordnance Survey). However, since accurate dating was not available to me at the time, separate records were not kept of the original and modern parts of any ancient woods other than Hayley and Madingley. Evidence of migration of molluscs into the Triangle of Hayley Wood (Paul 1978, p. 286) suggests that such a distinction is of little consequence since many molluscs apparently colonize such new additions to the old woods relatively rapidly. Records from all woods are presented in Table 1.



Fig. 1. A map to show the location of the woods visited during this study.

ANCIENT WOODS

The ancient woods of the area which I visited (Fig. 1) can be further subdivided into three categories on the basis of their flora, which probably reflects their management history. Hayley Wood, a brief account of which was given in part 1 (Paul 1975) and for which most information exists (Rackham 1975), may be taken as characteristic of typical well-preserved ancient woods. They have large 'standard' trees of oak (*Quercus robur*) and Ash (*Fraxinus excelsior*) with an understorey of coppiced ash, hazel (*Corylus avellana*) and hawthorn (*Crataegus oxyacanthoides*) and a very rich ground flora which includes several rarities. In some woods the oxlip (*Primula elatior*) is a characteristic ground herb, but it is replaced by the more common primrose (*P. veris*) in others. These woods yield the best mollusc fauna (24.7 species on average, excluding Hayley Wood with 35 species). Their fauna includes such rarities for Cambridgeshire as *Azeca goodalli*, *Arion subfuscus* and *Limax marginatus*, all three of which were first recorded for the county in Hayley Wood. The woods which I visited that fall into this category (A in Table 1) are as follows:- Hayley, Eversden, Madingley, Hardwick, Kingston and Gransden Woods.

Two of the ancient woods visited, Eltisley and Potton, are owned by the Forestry Commission. Eltisley had already been entirely cleared, except for elm (*Ulmus* sp.) and replanted with conifers, the largest of which were 3–4m high in 1971. At that time the parts of the wood with the youngest conifers had a ground flora and mollusc fauna little more seriously affected than would have occurred under normal coppicing or clearance, but the parts with the tallest trees were already seriously impoverished and one can predict that little, if any, of the ancient wood flora and fauna will remain once the conifers form a dense canopy and acidify the soil. Potton Wood was in the process of being cleared in 1971 and will probably soon follow Eltisley Wood in becoming a sterile plantation. It is tragic that the character of these woods,

PAUL: MOLLUSCA OF ANCIENT WOODLAND

TABLE 1.
OCCURRENCE OF MOLLUSCS IN ANCIENT AND MODERN WOODLAND

SPECIES	WOODS														T1	T2
	A						B		C		D		E			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14		
<i>Pomatias elegans</i> (Müller)	—	p	—	—	—	—	—	—	—	—	—	—	—	—	1	—
<i>Carychium minimum</i> Müller	p	—	—	—	p	p	—	p	—	p	—	—	p	—	5	1
<i>C. tridentatum</i> (Risso)	p	p	p	p	—	p	—	p	p	—	—	—	p	p	7	2
<i>Aplexa hypnorum</i> (L.)	—	—	—	—	—	—	—	—	—	p	—	—	—	—	1	—
<i>Lymnaea truncatula</i> (Müller)	p	—	—	—	—	—	—	d	p	p	—	—	—	—	4	—
<i>L. peregra</i> (Müller)	—	—	—	—	—	—	—	—	—	p	—	—	—	—	1	—
<i>Anisus leucostoma</i> (Millet)	d	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
<i>Azeca goodalli</i> (Férussac)	p	p	—	p	—	—	—	—	—	—	—	—	—	—	3	—
<i>Cochlicopa lubrica</i> (Müller)	p	p	p	p	p	p	p	p	p	p	p	p	p	p	10	4
<i>Columella edentula</i> (Draparnaud)	p	p	—	—	—	—	—	p	—	—	—	—	—	—	3	—
<i>Vertigo pygmaea</i> (Draparnaud)	—	d	—	—	—	—	—	—	—	—	—	—	—	—	1	—
<i>Lauria cylindracea</i> (Da Costa)	d	—	—	—	—	—	—	—	—	—	—	p	—	—	1	1
<i>Acanthinula aculeata</i> (Müller)	p	p	—	p	—	p	—	—	—	—	p	—	p	p	4	3
<i>Punctum pygmaeum</i> (Draparnaud)	p	p	—	p	—	p	p	p	—	—	—	p	p	—	6	2
<i>Discus rotundatus</i> (Müller)	p	p	p	p	p	p	p	p	p	—	p	—	p	p	9	3
<i>Arion ater</i> (L.)	p	—	p	p	p	p	p	p	p	p	—	p	—	p	9	2
<i>Arion subfuscus</i> (Draparnaud)	p	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
<i>Arion circumscriptus</i> Johnston	p	—	p	p	—	p	—	p	p	p	p	p	p	p	7	4
<i>Arion silvaticus</i> Lohmander	—	—	—	—	—	p	—	—	—	—	—	—	—	—	1	—
<i>A. hortensis</i> Férussac Agg.	p	p	p	p	p	p	p	p	p	p	p	—	p	p	10	3
<i>A. hortensis</i> Férussac form A.	—	—	p	p	—	—	—	—	—	—	—	—	—	—	2	—
<i>A. intermedius</i> Normand	p	p	p	p	p	p	p	p	—	—	—	p	p	p	8	3
<i>Vitrina pellucida</i> (Müller)	p	p	d	p	—	p	p	p	—	p	p	p	p	p	8	4
<i>Vitrea crystallina</i> (Müller)	p	p	p	p	p	p	p	p	—	—	p	p	p	p	8	4
<i>V. contracta</i> (Westerlund)	—	—	—	p	—	—	—	—	—	—	—	—	—	—	1	—
<i>Nesovitrea hammonis</i> (Ström)	p	p	—	p	—	p	p	p	—	—	—	d	p	p	6	3
<i>Aegopinella pura</i> (Alder)	p	p	p	p	p	p	p	—	—	p	p	—	—	p	8	2
<i>A. nitidula</i> (Draparnaud)	p	p	p	p	d	p	p	p	p	p	p	p	p	p	10	4
<i>Oxychilus cellarius</i> (Müller)	p	p	—	p	p	p	p	p	p	p	p	p	p	p	9	4
<i>O. alliarius</i> (Miller)	p	d	p	p	p	p	—	—	p	—	p	p	p	p	7	4
<i>O. helveticus</i> (Blum)	p	p	p	p	p	p	p	—	—	—	p	p	p	p	7	4
<i>Milax budapestensis</i> (Hazay)	—	—	—	—	—	—	—	—	p	—	—	—	—	p	1	1
<i>Limax maximus</i> L.	p	—	p	p	—	—	p	—	p	p	—	p	—	p	6	2
<i>L. marginatus</i> Müller	p	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
<i>Deroceras laeve</i> (Müller)	p	p	—	—	p	—	—	—	—	—	p	p	p	p	3	4
<i>D. reticulatum</i> (Müller)	p	p	p	p	p	p	—	—	p	p	p	—	—	p	8	2
<i>Euconulus fulvus</i> (Müller)	p	p	—	p	p	p	p	d	—	p	—	—	p	p	8	2
<i>Cochlodina laminata</i> (Montagu)	p	p	p	p	p	p	p	p	—	—	p	—	p	p	8	3
<i>Clausilia bidentata</i> (Ström)	m	p	p	p	p	p	—	p	—	p	p	—	—	p	8	2
<i>Monacha cantiana</i> (Montagu)	m	—	m	—	m	—	dm	—	—	d	—	—	—	—	(5)	—
<i>Trichia striolata</i> (Pfeiffer)	—	dm	m	—	—	dm	—	—	—	—	d	—	—	—	(3)	1
<i>T. plebeia</i> (Draparnaud)	p	p	—	p	—	p	p	p	p	p	—	p	p	—	8	2
<i>T. hispida</i> (L.)	—	—	—	—	—	—	—	—	—	—	—	—	—	p	—	1
<i>Cepaea nemoralis</i> (L.)	p	—	—	p	—	d	p	d	—	d	d	d	d	p	6	4
<i>C. hortensis</i> (Müller)	p	p	p	d	p	d	—	d	—	—	—	—	—	p	7	1
<i>Pisidium personatum</i> Malm	p	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
<i>P. obtusale</i> (Lamarck)	p	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Number of visits	65	6	5	4	1	2	3	1	1	1	2	2	7	5	—	—
Total live species	35	24	20	27	18	24	18	18	14	17	16	15	20	26	—	—
Mean number of live species	24.7						18.0		15.5		15.5		23.0			

p = present alive, d = dead shells only, m = marginal only.
1 Hayley Wood, 2 Evesden, 3 Madingley Wood (ancient core only), 4 Hardwick, 5 Kingston, 6 Gransden, 7 Potton, 8 Eltisley, 9 Papworth, 10 Overhall Grove, 11 The Belts, 12 A45 Wood, 13 The Triangle of Hayley Wood, 14 18–19th Century additions to Madingley Wood. T1 = frequency of occurrence in ancient woods (1–10), T2 = frequency of occurrence in modern woodland (11–14).

which has probably remained essentially unchanged for at least 1000 years, should be destroyed so quickly. In 1971 the mollusc fauna was still quite healthy with 18 species recorded for both woods.

Two more small patches of ancient woodland had also been changed in character at some time. Papworth Wood and Overhall Grove are largely or entirely dominated by elm and have a high (c. 1m) ground flora of grasses, goosegrass (*Galium aparine*), nettles (*Urtica dioica*) and brambles (*Rubus fruticosus* agg.). The elm dominated parts of these woods show no coppice structure, few, if any, standard trees and, since the elms are very close together, have either been completely cleared and allowed to regrow (Papworth Wood) or are modern additions to older woodland (Overhall Grove). The mollusc fauna of these two ancient woods may not seem to differ from those of other ancient woods judged by Table 1, which only records presence or absence of species, but it is impoverished (15.5 species on average) and the relative abundances of species differ. In both woods population densities of all species are low and many of the commonest species in typical ancient woods are distinctly rare. For example, *Discus rotundatus* is widespread and abundant in other ancient woods, but only a single specimen, practically the last recorded, was found in Papworth Wood and none at all in Overhall Grove. *D. rotundatus* and *Cochlodina laminata* seem to avoid elm wood. The latter was not found in either Papworth Wood or Overhall Grove.

MODERN WOODLAND

Records of molluscs were taken from The Belts, near Eversden Wood, and a small patch of wood on the north side of the A45 road near Hardwick Hall (National Grid Reference 52/377596). In addition separate records were kept of the 18th and 19th century additions to Madingley Wood and the Triangle, a 20th century addition to Hayley Wood (see Paul 1978, p. 292). Neither The Belts nor the A45 wood has the typical ground flora of the ancient woods. Ivy (*Hedera helix*) and wood sanicle (*Sanicula europaea*) are the most common herbs. The fauna of these modern woods is poor (15.5 species on average) and includes the most catholic elements of the ancient wood fauna, such as *Cochlicopa lubrica*, *Arion hortensis* agg. and *Aegopinella nitidula* which are generally widespread and by no means confined to woodland. A few typical woodland species like *Acanthinula aculeata*, *Cochlodina laminata*, *Arion circumscriptus* s.s. and *Limax maximus* occur, but virtually no new elements. *Lauria cylindracea*, found alive in the A45 wood and *Trichia hispida* from Madingley, are the only species found living in modern, but not ancient, woodland. The lack of *T. hispida* in the core of Madingley Wood could easily be due to oversight.

DISCUSSION

A few additional species have been recorded from the woods of Table 1, but are either represented by solitary dead shells or are confined to the margins of the woods. The only major omission from the table is the fauna of the old chalk pit in Madingley Wood which contains several species not found in the wood itself. Again these are not typical of woodland environments.

As far as the original aim of detecting an ancient Atlantic forest mollusc fauna is concerned (see Kerney 1966 for comments on the likely composition), some suggestions do emerge. The fauna of the ancient woods in Table 1 includes perhaps four categories of molluscs. First some freshwater or extremely hygrophilous species which survive in streams and pools in these predominantly wet woods. *Lymnaea truncatula*, *L. peregra*, *Anisus leucostoma*, *Aplexa hypnorum*, *Deroceras laeve* and *Pisidium* spp. belong here. Next there are some almost ubiquitous species, typified by *Cochlicopa lubrica* and *Aegopinella nitidula* which were found in every single wood

visited. Thirdly are common species which are characteristic of woodland in East Anglia. These include *Carychium tridentatum*, *Clausilia bidentata*, *Punctum pygmaeum*, *Arion circumscriptus*, *Euconulus fulvus*, *Oxychilus helveticus*, *Aegopinella pura*, *Vitrina pellucida* and even *Discus rotundatus*, which are widespread in other environments elsewhere in Britain. Finally there is a group of somewhat rarer species more closely confined to woodland in East Anglia, although again sometimes occurring in other habitats elsewhere in Britain. These include *Azeca goodalli*, *Columella edentula*, *Acanthinula aculeata*, *Cochlodina laminata*, *Trichia plebeia*, *Arion subfuscus*, *Limax maximus* and *L. marginatus*. The latter two categories intergrade somewhat and one or two species might equally well be transferred between them.

To some extent these categories may be interpreted. The aquatic species are obviously strongly associated with water. Several are marshland or opportunist species, e.g. *Pisidium personatum*, *Aplexa hypnorum* and *Anisus leucostoma*, which could well have survived in poorly drained parts of the original forest, but could equally well be modern colonists. The nearly ubiquitous species were probably widespread in the original forest and withstood clearance to survive in a variety of more artificial habitats. Species which are typical of, or confined to, woodland in East Anglia, may well be drought sensitive. East Anglia is one of the driest parts of Britain and many molluscs, particularly the larger slugs and hygrophilous species like *Columella edentula*, can probably only survive in areas where the humidity is kept high by a permanent canopy of vegetation. Mordan (1977, p. 61) gives useful comparisons between microclimates of woodland and grassland at Monks Wood, Huntingdonshire, which lies about 15km north of the most northerly wood included in this study. He also gives (in Steele and Welch 1973, pp. 266–7) a list of species occurring in ancient woodland at Monks Wood Nature Reserve all of which have been recorded from the woods studied in Cambridgeshire. Whether these species are rare or relatively common may reflect their sensitivity to human interference in addition to other environmental parameters. In some species, e.g. *Helicodonta obvoluta*, tolerance of human interference declines towards the edge of their range. The reverse, i.e. increasing association with human sites near the edge of the range, is also known to occur.

There remain some puzzling features of mollusc distribution which suggest that the original forest fauna may not have been uniform. Why, for example, is *Clausilia bidentata* absent from most of Hayley Wood when it occurs in 7 of the 9 other ancient woods visited? Why is *Trichia plebeia* replaced by a large form of *T. hispida* in at least part of Madingley Wood, and why is the latter the only site for *T. hispida* in all the woods visited whereas *T. plebeia* occurs in 9 of the 12 woods visited? These questions remain to be answered.

ACKNOWLEDGEMENTS

I am extremely grateful to the Cambridgeshire and Isle of Ely Naturalists' Trust for permission to work in Hayley Wood and to the Department of Zoology, Cambridge University for permission to work in Madingley Wood. Dr. Oliver Rackham provided historical information and stimulus for this study, while Dr. P. B. Mordan discussed many of the ideas and provided useful criticism of the manuscripts. Any errors are, however, entirely my own.

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REVIEW

Endodontid land snails from Pacific Islands (Mollusca: Pulmonata: Sigmurethra). Part 1 Family Endodontidae. By Alan Solem. 508 pp (quarto), 208 figures. Field Museum of Natural History, Chicago, 1977. Price \$31-50 (Approx. £19-00).

This handsomely bound volume contains a wealth of information about endodontid land snails. After brief introductory sections on previous studies and the material, the book continues with detailed accounts of the methods of study and patterns of morphological variation; the latter including both anatomy and shell morphology. Two sections on habitat range and extinction and on phylogeny and classification precede the main bulk of the book, the systematic review, in which 185 species and sub-species are described and excellently illustrated. A discussion of zoogeography, references, an appendix on anatomical terms and an index complete the work.

The section on patterns of morphological variation includes numerous graphs of measured shell parameters including two with accompanying line illustrations of the relevant shell shapes which render them much more immediately understandable. Scanning electron micrographs illustrate the range of surface micro-sculpture, apertural barriers and radular teeth, all of which are described in as much detail as gross shell characters. An apical sculpture of irregular microspirals and more prominent radial riblets is found to be characteristic of endodontid snails while charopids usually have broad spiral cords without any radial elements. The conclusion that apertural barriers are protective against arthropod predators seems inescapable. Even so predation of eggs by introduced species of ants is believed to have caused the extinction of some species.

The anatomy of endodontids and its variation is covered for all species dissected. Terminal male genitalia are characterized by various arrangements of pilasters within the penis, two being the usual number.

The section on phylogeny includes a useful summary diagram showing the evolutionary relationships between genera. This reveals that brood pouches in the umbilicus have developed independently in several lineages and their development partly accounts for the success of the Pacific Island endodontids. Not only does this practice provide the eggs and young with protection, but in the extreme cases of its development the offspring get a gratuitous supply of calcium carbonate from the parental shell; a useful adaptation to life in tropical rain forest leaf litter the principal habitat of endodontids, where carbonate is in short supply. In *Liberia fratercula*, from the Cook Islands, umbilical closure prevents the young from emerging through the umbilicus. The parent snail vacates the upper whorls of the spire and fills them with solid calcite. The young snails gnaw their way through the solid apex to emerge.

Solem concludes that three families are present in Pacific Islands; the Punctidae, the Endodontidae and the Charopidae. The systematic section contains a useful list of taxa in the Endodontidae (as defined by Solem) as well as summary lists for the Pacific Islands groups. I missed a distribution map however and hope that one will be included in the more detailed discussion of zoogeography promised in part 2. The outstanding feature of the systematic review is the excellent line illustrations which reveal the variety and beauty of these minute land snails. Of the 185 taxa treated, 102 are new, including the genera *Aaadonta* and *Zyzyxodonta*. [One suspects a desire on Solem's part to have his creations begin and end any list of genera. Actually should one so desire, it is possible to go two better. The Hawaiian vocabulary includes aa aa (for blocky lava) and there is an exit off the Las Vegas-Los Angeles Interstate near Death Valley called Zzyzx Road: presumably *the* last place on earth!]

The style is a little verbose in early sections. One wonders, for example, how 'judgement decisions' differ from either 'judgements' or 'decisions'. I found that the reproduction of the numerous tables and some graphs detracts from the appearance of the work. All the tables have been typed using an electric typewriter and then enlarged or reduced to fit page depth, page width or column width. The style of lettering is weak compared with the printed page and becomes obtrusive where it is enlarged. Graphs have received the same treatment and again where they have been enlarged they look heavy and clumsy (e.g. figs. 84–5, pp. 194–5). One other difficulty which I encountered was that in discussing morphological variation frequent reference is made to the figures in the systematic section, but not to the pages on which the figures appear. A minor point, but it was irritating to search repeatedly for the relevant figure. However, all these details pale into insignificance compared with the scientific content of this monograph. Solem has set a new standard for systematic treatments of molluscan groups. Future workers will be forced to consider many more aspects of the groups they treat if they are to maintain this high standard.

C. R. C. PAUL

INSTRUCTIONS TO AUTHORS

Authors of papers submitted for publication in the *Journal of Conchology* are urged to pay careful attention to the following notes. Any author who has difficulty in complying with these requests, or has queries concerning manuscripts, should consult the Hon. Editor **before** submitting a manuscript.

1. Manuscripts should be sent to the Publications Committee, c/o Dr. M. P. Kerney, Dept. of Geology, Imperial College, London, SW7 2AZ.

2. **Two** copies of all text and illustrations should be submitted. (A few years ago the entire copy for one issue of the *Journal* was lost in a mail robbery!). Authors are strongly recommended to retain a further copy for proof correction.

3. The text should be **fully revised**, typed **double spaced**, with wide margins (at least 1 inch), pages numbered consecutively and should conform in style to recent issues of the *Journal*. Titles should be concise and apposite, address(es) of author(s) should follow the title. Linear measures and weights should be metric and authorities for specific names should be given when first mentioned. Location of voucher material should be stated wherever possible. A brief, but informative, abstract should precede the main text.

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e.g.

ELLIS, A. E. 1926. *British snails. A guide to the non-marine Gastropoda of Great Britain and Ireland, Pliocene to Recent*. 275 pp., 14 pls., Oxford.

BROWN, P. and STRATTON, G. B. (Editors). 1965. *World list of scientific periodicals published in the years 1900–1960*. (4th Ed.) 3 vols. London.

For periodicals give full title of the article, title of the periodical abbreviated according to the World List (4th Ed.), volume number, page numbers and plates.

e.g.

WOODWARD, F. R. 1965. Monograph of the British Lower Tertiary Unionidae, with descriptions of three new species. *J. Conch., Lond.* **25**: 316–330, pls. 22–27.

GOULD, S. J. 1969. An evolutionary microcosm: Pleistocene and Recent history of the land snail *P. (Poecilozonites)* in Bermuda. *Bull. Mus. comp. Zool. Harv.* **138**: 407–532, 5 pls.

8. Authors may obtain copies of all papers (other than brief notes) at cost price if ordered from printers (address: Messrs. Willmer Brothers Ltd., 62–68 Chester Street, Birkenhead, England) when galley proofs are returned.

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ON THE STATUS OF *POTAMOMYA*
J. DE C. SOWERBY 1835
(BIVALVIA: MYOIDA)

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52 Little Paddocks, Ferring, Worthing, Sussex, BN12 5NH

and

T. PAIN

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(Read before the Society, 19 November 1977)

Abstract: The English Lower Tertiary fossil *Mya plana* J. Sow. 1814, often referred to *Erodona* Bosc 1802, lacks the distinctive erodoniid chondrophore and seems closer to *Mya*. It is, however, unlike other myids in having a pit or slot confluent with the resilifer in the beak of the right valve; which receives the beak of the left valve. This characteristic seems sufficient reason to retain the valid generic name *Potamomya* J. de C. Sow. 1835 for this fossil.

The generic name *Potamomya* (J. de C. Sowerby 1835) although by priority of publication based on the English Lower Tertiary bivalve *Mya plana* J. Sowerby 1814, was also applied by G. B. Sowerby (1842, figs. 498, 499) to a figured extant South American species of *Erodona* Bosc 1802 and for this reason was correctly listed in the synonymy of that genus by Dall (1896, p. 422). Reference of the English fossil species to *Erodona* by Newton (1891, p. 91) and others, formalized by Keen (1969, p. N698), implicitly accepted a taxonomic relationship proposed by G. B. Sowerby (1821, p. 220) and J. Sowerby (1822, p. 87; 1826, pp. 60–61) but never established. A preliminary comparison of fossil specimens with Recent *Erodona* species by the late Dr. L. R. Cox revealed 'important differences' which in his opinion would probably justify revival of the name *Potamomya* for the fossils (personal communication, 1965). This has since been done informally (*e.g.* British Museum Natural History, 1975, plate 14, figs. 3–5) but Dr. Cox's death left the matter still undiscussed. We have therefore compared representative specimens (Figure 1), presenting our observations and conclusions below.

Ten points of comparison are listed in Table 1 for extant species of *Corbula*, *Erodona* and *Mya*, and the English Lower Tertiary bivalve. From these it is apparent that *Corbula* and *Erodona* are closely allied, differing importantly only in (7). Since Keen (1969) has cited this difference as distinguishing the family Erodonidae from the Corbulidae, the lack of this character in the fossil excludes it from the Erodonidae. It is unlike typical Corbulidae in respect of (4), (5), (6) and (8). Conversely, it resembles *Mya arenaria* L. in respect of (4) and (8), and the largest adult specimens of the fossil somewhat resemble small specimens of *M. arenaria* in having a slight posterior gape (5). The fossils however have a distinctive character (10) not mentioned in the original description, but clearly shown in the British Museum Natural History's figures (1959, pl. 14, figs. 3–5), which sets them apart from other described myids.

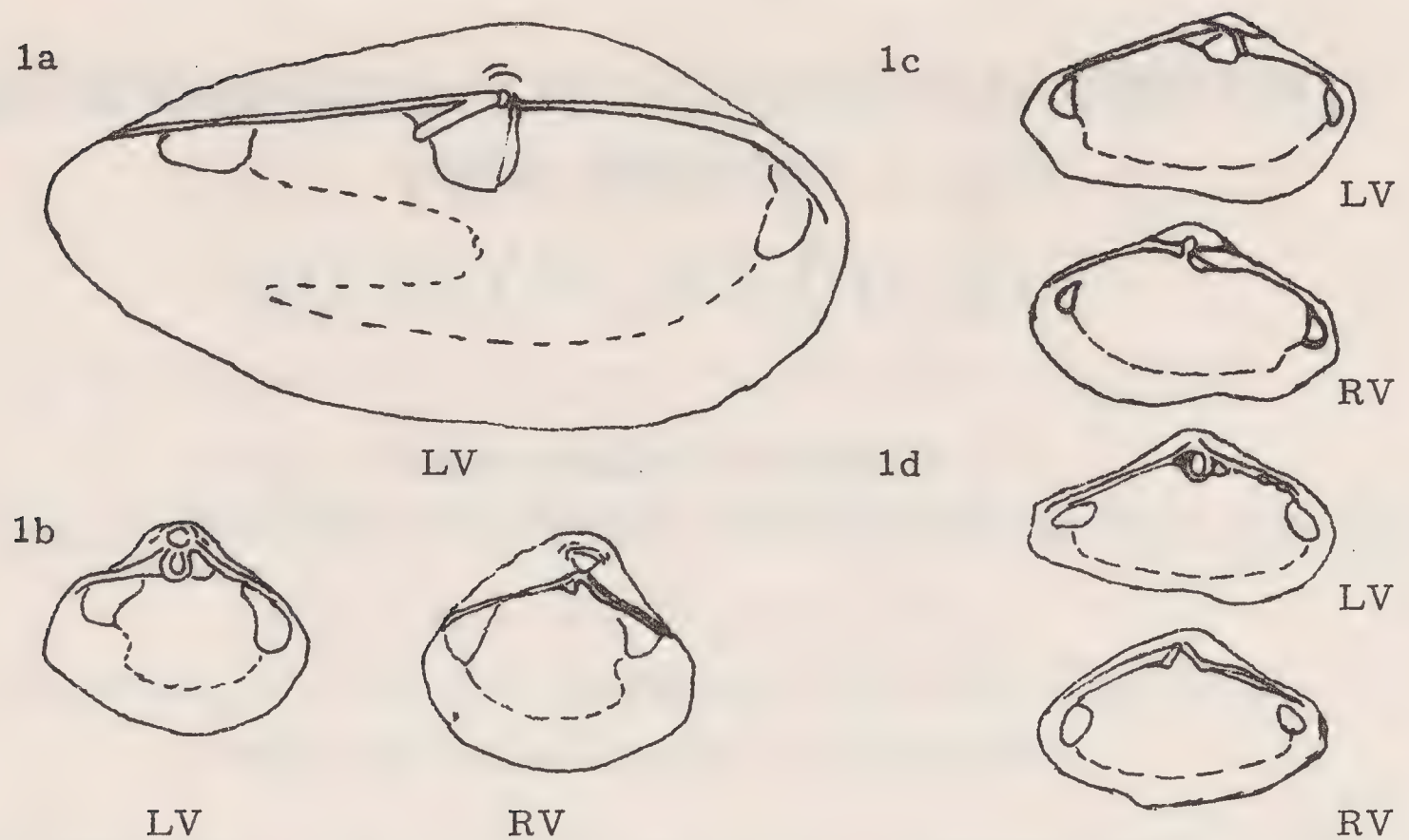


Fig. 1. Internal views of valves: 1a *Mya arenaria* L.; 1b *Corbula gibba* (Olivi); 1c *Mya plana* J. Sow.; 1d *Erodona mactroides* Bosc. (All approx. $\times 1\frac{1}{2}$.)

TABLE 1

Comparison of *Corbula gibba* (Olivi), *Erodona mactroides* Bosc, *Mya arenaria* L. and *M. plana* J. Sow. (*E. mactroides* from the Rio de la Plata estuary, Argentina; *M. plana* from the Lower Headon Beds (Upper Eocene), Hordle Cliff, Hampshire; other species from British coastal waters.)

	<i>C. gibba</i>	<i>E. mactroides</i>	<i>M. arenaria</i>	<i>M. plana</i>
1	Shell broadly triangular	Shell ovate-trapezoidal	Shell ovate	Shell ovate-triangular
2	Strongly inequivalve; RV larger than LV	As in <i>C. gibba</i>	Slightly inequivalve	As in <i>M. arenaria</i>
3	Umbo of RV higher than LV	Umbo of LV higher than RV	Umbo of RV slightly higher than LV	As in <i>M. arenaria</i>
4	Ventral edge of RV overlaps ventral edge of LV	Ventral edge of RV overlaps LV posteriorly	Ventral edges of valves meet	As in <i>M. arenaria</i>
5	No posterior gape	Slight posterior gape	Strong posterior gape	Slight posterior gape in largest adults
6	RV with deep triangular resilifer bordered by cardinal tooth-like ridges, the anterior projecting as a peg-like tooth	As in <i>C. gibba</i> (see 10) but lacks peg-like tooth	RV lacks teeth	RV with small anterior cardinal tooth-like ridge; shallow resilifer (see 10)
7	LV has solid projecting chondrophore bearing a deep triangular depression; a triangular pit anterior to the chondrophore receives peg-like tooth of RV	LV has broad spoon-shaped chondrophore bearing a deep oval depression; slight pit anterior to chondrophore; deep pits in front and behind receive cardinal tooth-like ridges of RV	LV with broad triangular projecting chondrophore; lacks anterior and posterior pits	LV with moderately broad triangular somewhat downward facing chondrophore.
8	Adductor muscle scars approximately equal in size and shape	As in <i>C. gibba</i>	Adductor muscle scars unequal in size and shape	As in <i>M. arenaria</i>
9	Pallial sinus shallow	Pallial sinus extremely shallow to absent	Pallial sinus deep	Pallial sinus shallow
10		Beak of RV pierced by hole confluent with resilifer; in adults almost hidden by umbo		Pit or slot confluent with resilifer in beak of RV receives beak of LV

Conclusion. The fossil bivalve originally described as *Mya plana* is not referable to either the Erodonidae or the Corbulidae, but has some weakly developed characters of the Myidae. A distinctive character (10) distinguishes it from other genera in that family and, in our opinion, justifies retention of the valid generic name *Potamomya* for this fossil species. A detailed study is now being undertaken.

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- ¹ See Griffin, F. J., 1939. *J. Soc. Biblphy. nat. Hist.* 1: 249.
- ² Publication dates of the *Mineral Conchology* from Cleavelly, J. R., 1974. *J. Soc. Biblphy. nat. Hist.* 6: 418–475.

LITTORINA ARCANA sp. nov.:
A NEW SPECIES OF WINKLE (GASTROPODA:
PROSOBRANCHIA: LITTORINIDAE)

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Littorina arcana sp. nov.

Diagnosis: *L. arcana* resembles *L. rudis* (Maton, 1797) in shell and penial characters but differs in reproducing oviparously. Pallial oviduct morphology is closely akin to that of (oviparous) *L. nigrolineata* Gray (1839) (see Sacchi, 1975). Individuals of *L. arcana* kept in aquaria have been observed to lay egg masses. The eggs were coloured pink during the early stages of development. Similar egg masses have been observed in rock crevices on the beach. It is thought probable that Seshappa's report (1947) of oviparity in rough winkles applies to this species.

Though there are no diagnostic differences in shape, sculpture or colour distinguishing shells of *L. arcana* and *L. rudis*, the shells of *L. arcana* are frequently of a markedly 'patula' type (Heller, 1975).

The range of variation seen in penial morphology is wide and intergrades with that seen in *L. rudis*, but typically penes of *L. arcana* are relatively shorter with penial glands more numerous and extending most of the length of one edge of the penis (excluding the tip).

The best diagnostic character of *L. arcana* is the position and extent of a field of ciliated tissue which is an elaboration of the mantle lying between the genital tract and the columellar muscle. In *L. rudis* it is comparatively extensive, often thrown into folds and approximates to a right-angled triangle in outline with the greatest area near the distal termination of the genital tract. In *L. arcana* the field is inconspicuous and approximates to an elongate oval in outline.

Zonation of the species at the type locality depends on the season but the adults are generally found in the *Pelvetia* and *Verrucaria* zones. In Anglesey *L. arcana* is commoner on more exposed shores.

A fuller description of *L. arcana* is in press (*J. Conch., Lond.* 30).

Distribution: Common in Anglesey, Wales. Records also from Scotland, Yorkshire, Eire and France.

Type material: Holotype British Museum (Natural History) Reg. No. BM 197823W, Paratypes Reg. No. BM 197824W

Type locality: Porth Swtan, Anglesey, Wales SH299892

This work was supported by a N.E.R.C. studentship.

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ON *TRITONIA MANICATA* DESHAYES, 1853,
A DENDRONOTACEAN NUDIBRANCH
(GASTROPODA, OPISTHOBRANCHIA) NEW
TO THE BRITISH FAUNA

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(Read before the Society, 17 December 1977)

Abstract: *Tritonia manicata*, a common Mediterranean nudibranch, is recorded for the first time from British waters. It is described and figured so that it may easily be distinguished from other British tritoniids.

Extensive sublittoral collections by scuba divers examining the Lundy Marine Reserve at the entrance to the Bristol Channel have included sixty-seven species of opisthobranch molluscs. One of five species of *Tritonia* obtained during this work has proved to be a new record for the British Isles. Only one specimen of this tritoniid was included in the total collection of several thousand opisthobranchs taken during the three years since July, 1975. Lundy Island is the most northerly location known for this species and is possibly at the very limit of the zoogeographical range. Concurrent studies on different benthic groups such as the Coelenterata (Hiscock 1974) have demonstrated that other Mediterranean species, rarely found around Britain, are capable of surviving in this very favourable environment. A full list of the opisthobranchs recorded for Lundy is included in a recent publication (Brown, in press).

Tritonia manicata Deshayes, 1853 (Fig. 1a-d)

[Synonyms: *Duvaucelia gracilis* Risso 1826, *Nemocephala marmorata* Costa 1867, *Candiella moesta* Bergh 1884]

MATERIAL

A solitary specimen, with a body length of 11 mm in life, was collected in July, 1976 from 'Jenny's Cove' on the west coast of Lundy (lat. 51° 10' 40"N, long. 04° 40' 40"W) at a depth of 12 m below chart datum. The animal was attached to an unidentified hydroid on granite bedrock. No alcyonaceans, such as the soft coral, *Alcyonium* or 'Dead Man's Fingers' which is the usual diet of three other British species of *Tritonia*, were in the immediate vicinity.

DESCRIPTION

The ground colour was a bright white due primarily to the opacity of the internal organs but reinforced by some surface pigment. The digestive gland was a pink mass visible within the body, posterior to the anus. A number of dark maroon spots were scattered over the dorsum

(Fig. 1a) but not arranged in any definite pattern. The oral veil bore six long finger-like papillae and one small unpaired digitation on the right side. The four pairs of pallial gills were faintly pink in colour. The genital opening on the right lateral surface (Fig. 1c) was just anterior to the

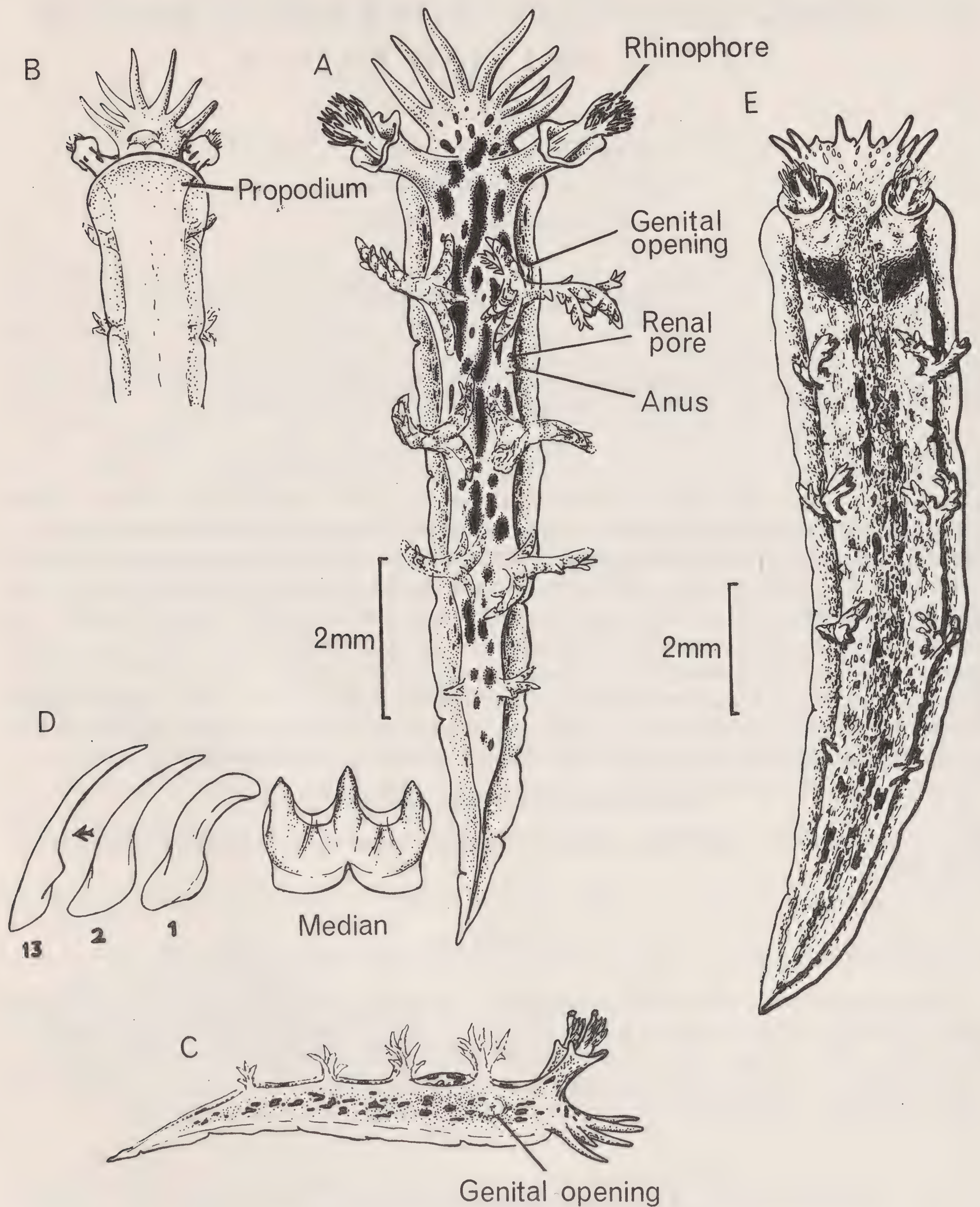


Fig. 1. a) *Tritonia manicata*, dorsal view of an 11 mm specimen from Lundy; b) anterior ventral view; c) right lateral view; d) camera lucida drawings of radular teeth taken from the 25th row; e) *T. plebeia*, dorsal view of a 14 mm specimen from Lundy.

level of the first pair of gills while the anus and renal pore lay near the right pallial margin between the first and second gill pairs. The flanks were dotted with maroon pigment in a similar density to those over the dorsum. The rhinophore sheaths appeared to be whiter nearest the uneven rims. The foot (Fig. 1b) was translucent and wider than the body. The propodium was smoothly rounded. The radula (Fig. 1d) of this 11 mm specimen had 33 rows and a maximum formula of 13.1.1.1.13. However, the radula ribbon widens as the animal grows, the first (oldest) row having only five teeth (1.1.1.1.1). The outer laterals were more slender than the inner laterals while the median tooth was triscuspid. The jaw plates bore numerous, closely-packed denticulations.

DISCUSSION

On the basis of coloration, external morphology and radular characteristics, there is no doubt that this British tritoniid is referable to *T. manicata* Deshayes 1853. Also I was able to compare it with a 10 mm specimen of *T. manicata* obtained while diving around the island of Ischia in the Bay of Naples, during a research visit to the Stazione Zoologica di Napoli in April, 1974.

Risso (1826) described a species (*Duvaucelia gracilis*) similar to this animal but Haefelfinger (1963) considered this inadequately brief description to be most likely a juvenile of *Mariona tethydea* (Delle Chiaje 1828) despite Pruvot-Fol's (1936) opinion that *D. gracilis* was synonymous with *T. manicata*. Some recent authors have chosen to follow Haefelfinger's nomenclature (Ros 1975) while others continue to follow Pruvot-Fol (Nordsieck 1972, Bouchet and Tardy 1976). Unfortunately the text of Deshayes (1853) has never been found but the illustration was carefully executed and corresponds somewhat better in appearance to the Lundy specimen than did Haefelfinger's range of animals. The latter's drawings and a photograph suggest a darker animal, the dorsal pigmentation being usually united into large patches. If all the published identifications are to be believed, the coloration varies between a yellowish or white body covered with black, brown, olive-green, dark-violet or maroon pigmentation in dots or patches. The shape, including the number of gills, is consistent throughout the literature. The size of the Lundy specimen is only one millimetre short of the maximum recorded length.

Five tritoniid species are now known from the British Isles: *T. hombergi*, *T. lineata*, *T. manicata*, *T. odhneri* and *T. plebeia*. The only one of the other four that could possibly be confused with *T. manicata* is *T. plebeia* (Fig. 1e) which is also mottled with dark pigment. Bouchet and Tardy (1976) consider that Labbé (1932) may have already made this mistake. The shape of the oral veil is consistently distinct, the papillae being relatively shorter in *T. plebeia*. Also the pigmentation over the dorsum is a dense mottling of brown, interrupted by white glistening specks. Very often in smaller specimens such as the 14 mm animal figured here (and equivalent to a large specimen of *T. manicata*), the brown coloration is particularly dark immediately behind the rhinophores. The dorsal pigmentation in *T. manicata* is rarely dense enough to obscure the distinctive pink digestive gland within the body. *T. odhneri* (Tardy 1963) also has six oral veil digitations and has only recently been recorded from the British Isles (Brown and Hunnam 1977). The colour, however, is the same bright pink as the gorgonacean (sea fan) diet, *Eunicella verrucosa*.

Tritonia manicata has been found on the Turkish coast of the Mediterranean Sea, in the Adriatic Sea (Trieste), in the Bay of Naples, along the French and Spanish Mediterranean coasts and along the Atlantic coasts of Morocco, France and now Britain. It was previously recorded as far north as Mor-Braz in Brittany (Bouchet and Tardy 1976, as *D. gracilis*) but this communication extends the known range northwards to the island of Lundy in the Bristol Channel. All records have been obtained from water less than 30 m in depth. Schmekel (1968) reports a diet of the alcyonacean, *Cornularia*, in the Bay of Naples.

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THE DIET OF *BUCCINUM UNDATUM* AND *NEPTUNEA ANTIQUA* (GASTROPODA: BUCCINIDAE)

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(Read before the Society, 17 December 1977)

Abstract: The prosobranch gastropods *Buccinum undatum* and *Neptunea antiqua* from the N.W. Atlantic have been regarded as food generalists, being largely opportunistic feeders upon carrion. However, examination of gut contents shows that polychaetes form about 60% of the diet of *Buccinum*, although a wide variety of other prey may be eaten. *Neptunea* has a more restricted diet and eats mainly bivalves, with polychaetes of lesser importance; although *Priapulus* formed a major part of its diet at Millport. The diets of these temperate species are broader than those of tropical relatives of similar size, and this pattern of high latitude food generalist and tropical specialist conforms with the general ecological hypothesis which suggests that the temporal heterogeneity of the environment at high latitudes precludes specialization upon a particular food type.

It is a common generalization that animals at high latitudes tend to have broader diets and habitat requirements than their equivalents in the tropics (Pianka 1966, McArthur 1972, Valentine 1973). The usual explanation of this phenomenon is that the temporal heterogeneity of the environment and the unpredictable food supply at high latitudes preclude extreme specialization upon one major food resource. By contrast, in the tropics, environments are more stable, food supply is more predictable and specialization has considerable advantages in efficiency. Most examples of latitudinal differences in food niche breadth have come from terrestrial ecosystems (e.g. Cody 1974, McArthur 1972), although there is some evidence from the marine gastropod *Conus* (Kohn 1966) and other predatory gastropods (Taylor and Taylor 1977), that diets are broader at high latitudes.

The prosobranch gastropod family Buccinidae constitutes one of the most diverse and important elements in high latitude marine molluscan faunas. For instance, they comprise 31% of gastropod species around East Greenland (Thorson 1944), 17% in Iceland (Thorson 1941), 35% around Arctic Canada (Macpherson 1971), and 23% around Antarctica (Powell 1951, as Buccinulidae). This contrasts with tropical faunas where species of Buccinidae usually comprise less than 3% of the species in any gastropod fauna (Taylor 1977).

High latitude Buccinidae, with their highly variable populations, have frequently been cited as examples of ecological generalists and their comparative success at these latitudes has been attributed to their broad habitat and food requirements which are considered to be adaptations to unpredictable resources (Valentine 1972). The northern Atlantic species *Buccinum undatum* Linnaeus must be the most studied species of Buccinidae and it is renowned for its opportunistic feeding habits upon carrion (Fretter and Graham 1963). However, most observations have been made in the artificial conditions of aquaria or baited traps and many other data are anecdotal in nature. Blegvad (1915), Hunt (1925) and Nielsen (1975), examined stomach contents of small samples of *Buccinum* and even though these studies suggest a more

specialized diet, there have been no observations upon the natural diet of whelks which are comparable to the quantitative work on some tropical predatory gastropod groups (Kohn 1959, 1968, 1970; Kohn and Nybakken 1975, Paine 1963, Taylor 1976, 1978). Similarly, *Neptunea antiqua* (Linnaeus) has been frequently cited as a scavenger, but Pearce and Thorson (1967) have shown that in experimental conditions the response to carrion is very weak and that gut samples suggest a diet of bivalves and polychaetes.

Thus, in order to investigate the ecological characteristics attributed to the high latitude Buccinidae, I have attempted in this study to determine the natural diets of *Buccinum undatum* and *Neptunea antiqua*, which are the two most accessible species of Buccinidae in the British fauna.

METHODS

Samples of *Buccinum undatum* were collected at Dunstaffnage Bay, Oban, in August 1975 and February 1976; at Burnham on Crouch, Essex, in January 1976; and along with *Neptunea antiqua* at Millport in October 1976.

The gastropod shells were cracked and the animals fixed in formalin immediately after collection, and the oesophageal, stomach, and rectal contents examined and identified microscopically. Sample size ranged from 48–171 specimens for *B. undatum* and 230 specimens for *N. antiqua*.

RESULTS

Buccinum undatum. The results of the gut content examinations for the three localities are shown in Tables 1–4. In general, only about 35% of the animals contained food items in the gut, and of these between 60–80% were identifiable. Many animals contained sediment only, and this was thought to be residual from the capture of food items. Similar low returns from stomach samples were recorded by Blegvad (1915), Hunt (1925) and Nielsen (1975).

TABLE 1

Food items recovered from the gut of *Buccinum undatum* at Oban August 1975.

Food items	Number of occurrences	% of Identifiable food items
<i>Lanice conchilega</i> (Pallas)	25	52.1
'nereid' setae	1	2.1
'eunicid' setae	1	2.1
crustacean eggs	5	10.4
brachyuran gill	1	2.1
amphipod fragments	1	2.1
<i>Balanus balanus</i> (Linnaeus)	5	10.4
<i>Cerastoderma edule</i> (Linnaeus)	1	2.1
bivalve gill	4	8.3
ascidian?	1	2.1
<i>Metridium senile</i> (Linnaeus)	3	6.3
Total sample	171	
Identifiable food items	48	
Indeterminate remains	11	
Food diversity index *D	14.59	

$^*D = \sum \lg p_i$ where p_i 's are the frequencies of occurrence of the various prey items (Herrera 1976).

TABLE 2

Food items recovered from the gut of *Buccinum undatum* at Burnham on Crouch January 1976

Food items	Number of occurrences	% of identifiable food items
<i>Lanice conchilega</i> (Pallas)	8	22.2
<i>Eunereis longissima</i> (Johnston)	3	8.3
<i>Gattyana cirrosa</i> (Pallas)	2	5.6
<i>Eunoe nodosa</i> Sars	1	2.8
<i>Lysidice ninetta</i> Audouin & Milne-Edwards	1	2.8
<i>Neoamphitrite figulus</i> (Dalyell)	1	2.8
<i>Amphitritides gracilis</i> (Grube)	1	2.8
<i>Pista maculata</i> (Dalyell)	1	2.8
<i>Sthenelais boa</i> (Johnston)	1	2.8
'terebellid' setae	4	11.1
'nereid' setae	1	2.8
'eunicid' setae	1	2.8
indeterminate setae	3	8.3
<i>Aspidosiphon mulleri</i> Diesing	2	5.6
<i>Buccinum undatum</i> Linnaeus	1	2.8
gastropod fragments?	3	8.3
Cirripede fragments	1	2.8
crustacean eggs	1	2.8
Total sample	128	
Identifiable food items	36	
Indeterminate remains	9	
Food diversity index D =	22.74	

TABLE 3

Food items recovered from the gut of *Buccinum undatum* at Millport 1976.

Food items	Number of occurrences	% of identifiable food items
<i>Aphrodite aculeata</i> Linnaeus	9	47.4
<i>Amphicteis gunneri</i> (Sars)	2	10.5
<i>Chaetopterus variopedatus</i> (Renier)	1	5.3
unidentified setae	2	10.5
<i>Priapulus caudatus</i> Lamarck	2	10.5
brachyuran fragments	3	15.8
Total sample size	48	
Identifiable food items	19	
Indeterminate remains	12	
Food diversity index D =	5.34	

It is at once clear that polychaetes are the most important prey item for *Buccinum*, comprising 85% of the identifiable food items of the sample from Burnham, 54% of the summer sample at Oban and 74% of the sample at Millport. The sand-tube dwelling polychaete, *Lanice conchilega* (Pallas), is by far the most common single food item at Dunstaffnage where it comprises 50% of the identifiable items. However, at Burnham, although *Lanice* is the most frequently eaten polychaete, at least nine other species are taken, including both errant and sedentary forms. At Millport, *Aphrodite*

TABLE 4

Food items recovered from the gut of *Buccinum undatum* at Oban
February 1976.

Food items	Number of occurrences	% of identifiable food items
Simple ascidian (<i>Ascidiella</i> ?)	50	92.6
<i>Nephtys caeca</i> Fabricius	1	1.9
brachyuran gill	2	3.7
egg capsules	1	1.9
Total sample	128	

aculeata is surprisingly the most common prey item, accounting for 47% of the identifiable food items, with three other polychaete species of lesser importance. Other prey items from the three localities include the sipunculid *Aspidosiphon*, barnacles, crustacean eggs, the anemone *Metridium*, the bivalve *Cerastoderma edule*, the priapulid *Priapulus caudatus* and also a single specimen from Burnham containing a complete radula ribbon of *Buccinum undatum*. It is probable that some of the stomach contents, such as the brachyuran fragments, were from dead, moribund or moulting animals, but it is clear that many of the other items were taken as whole live prey.

The sample from Oban in January (Table 4) shows a rather different set of food items, the majority of whelks with food in their stomachs contained material probably from the ascidian *Ascidiella*, with only one polychaete and some pieces of crab gill. This sample suggests some seasonal changes in the diet of the whelk, but huge samples would be necessary to determine any seasonal pattern.

Neptunea antiqua. A large proportion of the Millport sample of *Neptunea* had empty stomachs and of those that contained material, this in many cases consisted of sediment or small pieces of unidentifiable organic material (Table 5). These fragments are probably in the main small

TABLE 5

Food items recovered from the gut of *Neptunea antiqua* at Millport October 1976.

Food items	Number of occurrences	% of identifiable food items
Indeterminate bivalve fragments	37	51.4
<i>Abra alba</i> (Wood)	9	12.5
<i>Priapulus caudatus</i> Lamarck	17	23.6
<i>Aphrodita aculeata</i> Linnaeus	2	2.8
<i>Terebellides stroemi</i> (Sars)	1	1.4
<i>Glycera</i> sp.	1	1.4
brachyuran fragments	2	2.8
Axiidae fragments	1	1.4
fish scales	1	1.4
brown tubes	1	1.4
Total sample	230	
Identifiable remains	72	
Indeterminate material and sediment	35	
Food diversity index D =	12.16	

macerated pieces of prey items recorded in the table and it is unlikely that any major prey category has gone unrecorded. Similar low returns of gut contents were recorded by Blegvad (1915), and Pearce and Thorson (1967) concluded from their experimental work that the food consumption of *Neptunea* is very modest.

Fragments of bivalves, especially pallial margins, feet, siphons and pieces of periostracum, make up the bulk of the identifiable material from the stomach samples. Some of these fragments can be matched with *Abra alba*, whilst in most other cases, although *Abra* is the most likely prey, the poor state of the fragments precludes further identification. The priapulid, *Priapulus caudatus*, is surprisingly the second most frequent prey item; however it is likely that its importance in the diet at Millport is a local effect, for although *Priapulus* is moderately common in the muddy sediments of this area, it is not as abundant in other places (A. Ansell personal communication reports densities of *P. caudatus* around Millport of approximately 3.3/m² but as high as 23/m²). Interestingly, this is the first record of *Priapulus* being eaten by another invertebrate, and *Priapulus* itself is a predator upon polychaetes such as *Aphrodite* and *Nephtys* (Land 1970). Polychaetes form only a small part of the diet of *Neptunea* and include *Aphrodite*, *Terebellides* and *Glycera*. The only other food consists of crustacean fragments.

TABLE 6

List of all food items recorded for *Buccinum undatum*

T = Taylor, this paper; B = Blegvad (1915); H = Hunt (1925); Han. = Hancock (1960); D = Dakin (1912); N = Nielsen (1975); R = Riser (1969).

Aq. denotes aquarium observations.

Nomenclature and classification of polychaetes after Hartman (1959)

Polychaeta

<i>Aphrodite aculeata</i> Linnaeus	T
<i>Eunoe nodosa</i> (Sars)	T
<i>Gattyana cirrosa</i> (Pallas)	T
<i>Sthenelais boa</i> (Johnston)	T
<i>Eunereis longissima</i> (Johnston)	T
<i>Nephtys caeca</i> Fabricius	T
<i>Nephtys</i> sp.	B
<i>Lysidice ninetta</i> Audouin and Milne-Edwards	T
<i>Lumbrinereis fragilis</i> (Müller)	B,H
<i>Chaetopterus variopedatus</i> (Renier)	T
<i>Arenicola marina</i> (Linnaeus)	B
'maldanids'	N
<i>Pectinaria belgica</i> (Pallas)	B
<i>Amphicteis gunneri</i> (Sars)	T
<i>Amphitritides gracilis</i> (Grube)	T
<i>Artacama proboscidea</i> Malmgren	B
<i>Lanice conchilega</i> (Pallas)	T
<i>Loimia</i> sp.	H
<i>Neoamphitrite figulus</i> (Dalyell)	T
<i>Pista maculata</i> (Dalyell)	T
<i>Chone duneri</i> Malmgren	N

Gastropoda

<i>Acmaea testudinalis</i> Müller	Aq.,R
<i>Crepidula fornicata</i> (Linnaeus)	Aq.,Han.
<i>Buccinum undatum</i> Linnaeus	T,B,N
<i>Neptunea antiqua</i> (Linnaeus)	B

Bivalvia

<i>Nucula nitidosa</i> Winckworth	Aq.,N
<i>Nuculana pernula</i> (Müller)	Aq.,N
<i>Modiolus modiolus</i> (Linnaeus)	N
<i>Mytilus edulis</i> Linnaeus	Han.

<i>Pecten maximus</i> (Linnaeus)	Aq.,D
<i>Ostrea</i> sp.	Aq.,Han.
<i>Cerastoderma edule</i> (Linnaeus)	T,N,Han
<i>Parvicardium scabrum</i> (Philippi)	Aq.,N
<i>Spisula elliptica</i> (Brown)	Aq.,N
<i>Spisula subtruncata</i> (da Costa)	Aq.,N
<i>Cultellus pellucidus</i> (Pennant)	Aq.,N
<i>Abra</i> sp.	B
<i>Mya arenaria</i> Linnaeus	Aq.,Han.
Malacostraca	
Amphipod fragments	T
<i>Nephrops</i> dead	Aq.,D
<i>Eupagurus</i> sp.	H
brachyuran fragments	T
decapod eggs	T
Cirripedia	
<i>Balanus balanus</i> Linnaeus	T
Echinoidea	
<i>Echinocyamus pusillus</i> (Müller)	H,B
Sipunculoidea	
<i>Aspidosiphon mulleri</i> Diesing	T
Priapulidae	
<i>Priapulus caudatus</i> Lamarck	T
Anthozoa	
<i>Metridium senile</i> (Linnaeus)	T
Ascidacea	
<i>Ascidella</i> ?	T
Vertebrata	
Flatfish	Petersen, 1911

DISCUSSION

The total range of organisms upon which *Buccinum undatum* has been reported as feeding is shown in Table 6. This shows a considerable diversity of prey items with at least 35 species from 10 major prey categories reported as being eaten under normal conditions; a further small number of prey species is listed as being eaten under experimental conditions. It is clear that *Buccinum* will take weakened or moribund prey when available; dead crabs are used as bait in whelk traps, and Petersen (1911) records *Buccinum* feeding upon flatfish trapped in nets. Furthermore, the observations of many workers, including Fretter and Graham (1963), Pearce and Thorson (1967), and Nielsen (1975) confirm the attractiveness of carrion to whelks. Nevertheless, it is also clear that under natural conditions polychaetes form the main food of *Buccinum*, with Crustacea and other molluscs as items of lesser importance. It is possible that some of the more active polychaetes in the list represent unhealthy or moribund animals, but the sedentary polychaetes such as *Lanice* are undoubtedly taken in a live and healthy condition. Nielsen (1975) has demonstrated that with the exception of *Cerastoderma*, *Buccinum* is unable to open healthy bivalves. However it can attack and open *Cerastoderma* by wedging the outer lip of its shell between the valves of the prey. *Cerastoderma* is a common prey of *Buccinum* in some sandy, sublittoral-fringe habitats, but the two species do not generally coexist.

A similar table of food items for *Neptunea antiqua* (Table 7), whilst not as extensive, shows a diversity of animals, with bivalves and polychaetes as the main prey categories taken. Pearce and Thorson (1967) reviewed the evidence from a number of workers, including Fänge (1958), for the use of a toxic salivary secretion to immobilize prey, and concluded that although this feeding mechanism is possible, their own experiments were inconclusive.

Feeding records from other Buccinidae from other parts of the world are rather scarce. The main prey of *Colus stimpsoni* in New England is *Littorina littorea*, although *Polynices*, damaged bivalves, moulting hermit crabs, egg capsules and carrion are also eaten (Riser 1969, West

TABLE 7

List of all food items recorded for *Neptunea antiqua*.

T = Taylor, this paper; B = Blegvad (1915); F = Fange (1958); PT = Pearce and Thorson (1967); P = Petersen and Jensen (1911).

Aq. denotes aquarium observations.

Polychaeta	
<i>Aphrodite aculeata</i> Linnaeus	T
<i>Nephtys</i> sp.	B
<i>Glycera</i> sp.	T
<i>Lumbrinereis fragilis</i> (Müller)	PT,Aq.
<i>Ophelia borealis</i> Quatrefages	PT,Aq.
<i>Amphitrite cirrata</i> Müller	PT,Aq.
<i>Pherua plumosa</i> (Müller)	PT,Aq. (as <i>Stylarioides</i>)
<i>Terebellides stroemi</i> (Sars)	T
Priapulioidea	
<i>Priapulus caudatus</i> Lamarck	T
Gastropoda	
gastropod eggs	B
Bivalvia	
<i>Mytilus edulis</i> Linnaeus	P,Aq.
<i>Abra alba</i> (Wood)	T
<i>Abra</i> sp.	B
indeterminate bivalves	T,B
Malacostraca	
Brachyuran fragments	T,F
Axiidae remains	T
Ascidiacea	
<i>Stylela</i>	B

1973). On the Pacific coast of the U.S.A., the small *Searlesia dira* has been the subject of a detailed study by Lloyd (1971). This whelk feeds upon a wide variety of food types but the dominant food is *Littorina* species which are taken live, and *Acmaea* which are usually moribund. Other food items include moribund and moulting crabs, live barnacles, weakened chitons, live polychaetes, bivalves, dead fish and dead echinoids. In New Zealand, *Penion adustus* feeds upon the bivalves *Dosinula* and *Prothaca*, whilst *Cominella* species prey upon the gastropods *Melagraphia* and *Lunella* as well as bivalves and carrion (Morton and Miller 1968). The small tropical species *Engina mendicaria* feeds upon sedentary polychaetes (Taylor, unpubl.).

It is well known that the Buccinidae are one of the most diverse gastropod families at high latitudes (Taylor and Taylor 1977), and Fig. 1 shows the increased importance of the Buccinidae among predatory gastropods on the eastern Atlantic shelf from about 40° northwards. Similar trends are seen on the continental shelves of other oceans, both in the northern and southern hemispheres. The Naticidae, Muricidae and Turridae are the only other predatory families of any importance at high latitudes, which is in sharp contrast to the situation in the tropics where 20–24 families of predators, containing many species, may coexist. Many of the tropical taxa are known to be specialized in diet; thus for instance the tropical species of the genus *Conus*, which have been extensively studied by Kohn (1959, 1968; Kohn and Nybakken 1975), divide into three main groups, which prey upon polychaetes, molluscs and fish, respectively, with each species in a group feeding upon a relatively narrow range of prey items. Similarly, species of Mitridae specialize upon sipunculid worms (Kohn 1970, Taylor 1976, 1978), the Terebridae upon polychaetes (Miller 1970), the Cassidae upon echinoids (Moore 1956, Hughes and Hughes 1971) and the Vasidae upon polychaetes and sipunculids (Taylor 1978). Groups of closely similar species which coexist in the same habitats, for instance as in the Muricidae (Taylor 1976, 1978) or the Conidae, exhibit a sharp partitioning of the prey species eaten.

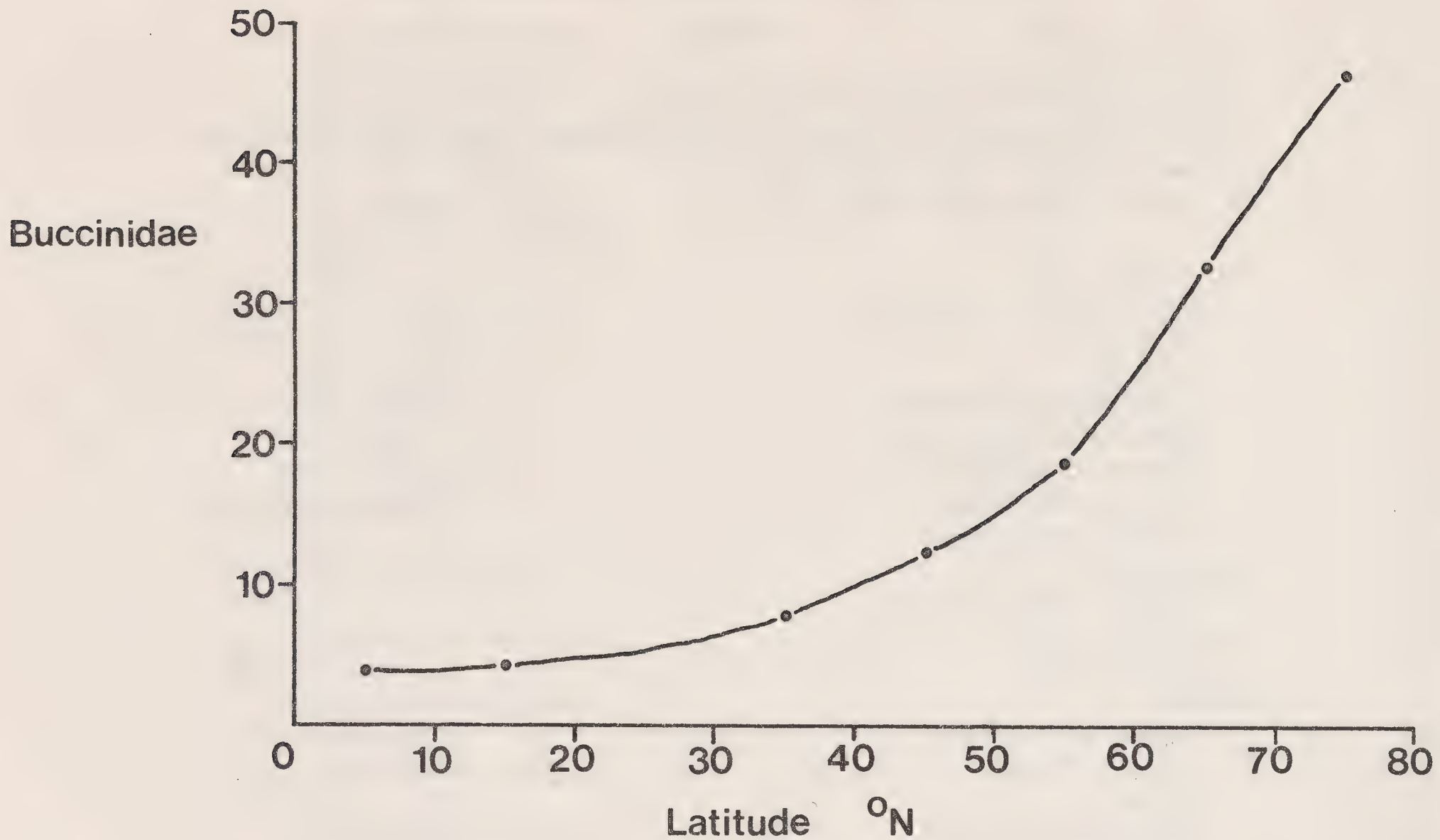


Fig. 1. Increased importance of Buccinidae with latitude along the eastern Atlantic shelf expressed as percentage of total predatory species for 10° latitude increments. Data from sources listed in Taylor and Taylor (1977).

There is some evidence of broadening of diet with latitude in some groups of gastropods. Thus Kohn (1966) shows clearly how *Conus californicus*, the only *Conus* species occurring in southern California, has a much broader diet than any of the group of sympatric species he studied on Hawaii. There are no real tropical counterparts of the northern buccinid species, for most tropical members of the family such as *Engina* are small and not obviously related to the northern genera. However, the families Fasciolaridae and Melongenidae are tropical families broadly related to the Buccinidae and contain species of a comparable size to *Buccinum* and *Neptunea*. Paine (1963) has documented the diets of some species from Florida and shows that most species are relatively specialized upon other molluscs, but that smaller species also eat sedentary polychaetes. The food diversity index (Table 8) calculated from Paine's data gives high values for the Florida species, comparable for those of *Buccinum*, but the range of major prey classes taken by the tropical species is far fewer. This suggests a greater flexibility of feeding behaviour by the temperate species.

The pattern of high latitude generalist and tropical specialist animals is well known and the phenomenon has been attributed to a response to the fluctuating predictability of the food resources at high latitudes caused by the strong seasonality of the environment. Taylor and Taylor (1977) present evidence that the distributional ranges of predatory gastropods are linked to the stability of the production cycle; there being a large increase in the diversity southwards of 40°N, where there is a change-over from seasonal to continuous productivity regimes.

From this study it is apparent that *Buccinum* is heavily dependant upon polychaetes for food and is not quite such an opportunist scavenger as had previously been believed. Nevertheless a wide variety of food items is taken and the whelk is clearly a food generalist. *Neptunea* is not greatly attracted to carrion and the small number of data available suggest a rather more limited diet than *Buccinum*. In this connection, it would be of considerable interest to examine the habits of the many sympatric species of Buccinidae recorded from Arctic waters (Thorson

TABLE 8

Comparison of food diversity between some predatory gastropods from Florida (data from Paine 1963) and *Buccinum* and *Neptunea*

predator	food diversity D	number of major food types
Florida species		
<i>Fasciolaria hunteria</i>	17.54	4
<i>Fasciolaria tulipa</i>	21.89	1
<i>Pleuroploca gigantea</i>	8.28	2
<i>Busycon contrarium</i>	13.62	1
<i>Busycon spiratum</i>	7.93	2
British species		
<i>Buccinum undatum</i> (Burnham)	22.74	5
<i>Buccinum undatum</i> (Oban)	14.59	7
<i>Neptunea antiqua</i> (Millport)	12.16	4

1944, Macpherson 1971, Odhner 1915, Matveeva 1975). If, as might be predicted, these species are food generalists, then it might also be expected that there should be habitat separation between the species. From an inspection of habitat data in expedition reports (Thorson 1944, Odhner 1915) this seems to be the case, but more detailed examination of the habits of these species is necessary.

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EFFECTS OF ATMOSPHERIC POLLUTION ON THE DISTRIBUTION OF *BALEA PERVERSA* (LINNAEUS) (PULMONATA:CLAUSILIIDAE) IN SOUTHERN BRITAIN

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(Read before the Society, 18 February 1978)

Abstract: *Balea perversa* has decreased greatly in areas that have suffered atmospheric pollution. When living on trees it is commonest on species with basic or neutral bark. Evidence is presented that in a polluted area it occurs only on those trees with the most base-rich bark. This could be due directly to reduction of the pH of the bark by SO₂ from rainwater, to a secondary effect of that on the epiphytic flora, or to some combined effect.

The distribution map for *Balea perversa* published by Kerney (1976) (Fig. 1A) suggests that this species has now disappeared from parts of England where it occurred early this century. The map for *Clausilia bidentata* (Ström) (Fig. 1B) suggests that this species may also have decreased locally, especially in the north and west Midlands of England and the London area. These effects are apparently superimposed upon a pattern with both species being commoner in the west and south than in the north and east, perhaps due to climatic factors, while *C. bidentata* is commoner on chalk and limestone than other geological strata.

The regions in which these species have decreased are those that appear to have suffered most from atmospheric pollution. Hawksworth and Rose (1970, 1976), Ferry, Baddeley and Hawksworth (1973) and others have demonstrated the usefulness of lichen distribution as a means of monitoring atmospheric pollution over large areas. Hawksworth and Rose (1970, 1976) have published maps of the extent of pollution as judged from epiphytic lichens, one of which is reproduced here as Fig. 1C. In preparing this figure I have transferred the data to the ten kilometre squares of the National Grid so as to facilitate comparisons with maps for Mollusca. The small errors involved in doing this do not affect my general conclusions.

Counts of ten-kilometre squares occupied by *B. perversa* in the areas shown on the maps demonstrate that this species has suffered most contraction of range in areas where lichens have decreased most due to atmospheric pollution (Table I). There is no evidence that *B. perversa* has shown any general decrease in areas unaffected by atmospheric pollution. Inspection of the maps shows that *C. bidentata* has suffered obvious decreases only in areas of very severe atmospheric pollution.

The arboreal and rupestral slug *Limax marginatus* Müller might also have decreased in areas with severe atmospheric pollution (Fig. 1D), but records of this species from before 1961 are too few for separate analysis. However, there can be no doubt that *L. marginatus* has not decreased in polluted areas to the same extent as *B. perversa*.

The sulphur dioxide that is a major component of atmospheric pollution in Britain increases the acidity of rain water and, in consequence, it increases the acidity of tree bark. This and other factors are responsible for the decreased abundance and diversity of epiphytic lichens in polluted regions (LeBlanc and Rao 1975, Hawksworth and Rose 1976). It is uncertain whether

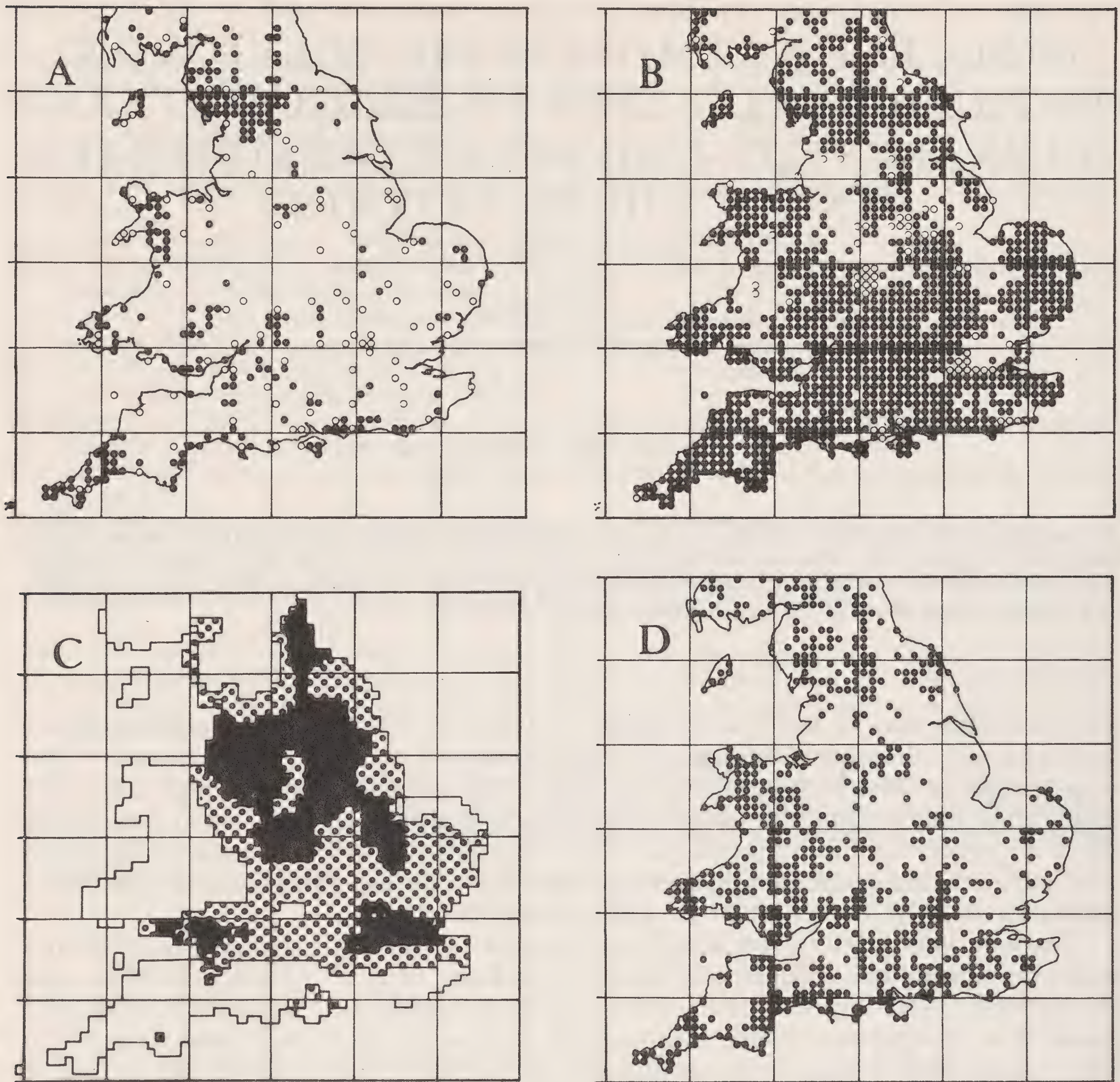


Fig. 1. Distribution of *Balea perversa* (A), *Clausilia bidentata* (B), and *Limax marginatus* (D), compared with the extent of atmospheric pollution as judged from epiphytic lichens (C). On maps A and B open points represent records obtained before 1961 (mostly 1876–1914) and closed points represent more recent records. On map D all records are represented by closed points. On map C lichen zones 8–10 (those with a richly varied lichen flora) are shown unshaded, zones 5–7 are represented by coarse stipple and zones 0–4 (greatly reduced lichen floras) by solid shading. Hawksworth and Rose (1976, pp. 30–31) explain the lichen zones in detail.

the decrease of *B. perversa* in polluted regions is due to reduced lichen abundance, increased acidity of tree bark or some combination of these effects. *B. perversa*, *C. bidentata* and *L. marginatus* all feed on lichens at times and they may all be found sheltering under, or amongst them, during dry weather. However, all three species sometimes occur on tree trunks or walls on which lichens are scarce or absent (personal observations).

Boycott (1921, 1934) and my own observations, show that in Britain *B. perversa* is never found on the trunks of pines (*Pinus*) or birches (*Betula*), that it is very uncommon on oaks (*Quercus*), but that it is often common on elms (*Ulmus*), hawthorns (*Crataegus*), elder (*Sambucus*

TABLE 1

Distribution of *Balea perversa* in southern Britain in relation to atmospheric pollution judged from epiphytic lichens. The analysis is of counts of ten kilometre squares of the National Grid, using data on *B. perversa* given in Fig. 1A and data on lichen distribution given in Fig. 1C. The 'lichen zones' are explained by Hawksworth and Rose (1976, pp. 30–31) and briefly in the caption to my Fig. 1.

	Lichen Zones		
	0–4	5–7	8–10
Total N of 10 km squares	350	609	757
squares with <i>B. perversa</i> recorded, since 1960	8 (2%)	69 (11%)	165 (22%)
squares with <i>B. perversa</i> recorded, pre-1960 only	17 (5%)	39 (6%)	43 (6%)
squares with <i>B. perversa</i> — all records	25 (7%)	108 (18%)	208 (27%)

nigra) and apple trees (*Malus*). Pines and birches have very acid bark, oaks have moderately acid bark, and elms, apple and especially elder have basic bark (Hawksworth and Rose 1976, personal observation). Likewise, when *B. perversa* lives on rocks and walls it is much commoner on basic (e.g. limestone, chalk, mortared brick), than on neutral or acid, substrates. *C. bidentata* shows a less marked preference for basic substrates, but it seems to avoid strongly acidic surroundings (cf. Boycott 1934). In contrast, *L. marginatus* occurs on the bark of a wide range of trees including pine and oak, as well as on low siliceous rocks in acid moorland (Boycott 1934, personal observations).

The preference for basic substrates shown by *B. perversa* in Britain is not reflected in its habitat preference in parts of southern Europe. Thus, at several localities near Bocognano, Corsica it was found living on and under boulders of acidic granite lying on slopes at 600–1000 m elevation in montane beech (*Fagus sylvatica*) woodland in April 1977. It has been shown that a number of other land snails are tolerant of a poorer supply of bases such as calcium in regions where the climate may be specially favourable (Boycott 1934, Kerney 1968, Cameron 1972). Blood calcium levels have recently been shown to affect tolerance of freezing temperatures in Mollusca (Murphy 1977), suggesting a mechanism accounting for increasing calciphile tendencies in colder regions.

An investigation of the local distribution and substrates occupied by tree-living *B. perversa* in part of Sussex, England in 1975–1977 is summarized in Fig. 2. Sites on walls were disregarded in this study, although a few of them are marked on Fig. 2. In this region the conurbation extending from Shoreham to Brighton is a source of atmospheric pollution and the pollution-sensitive lichen *Parmelia perlata* is absent there and in areas some distance downwind (Hawksworth and Rose 1976, Fig. 5-1). All nine of the sites on trees where *B. perversa* was found within five kilometres of the area from which *P. perlata* is absent were on elders, whereas 10 of 16 sites on trees beyond five kilometres were on other species (χ^2 , applying Yates's Correction = 12.45, 1 d.f., $p < 0.001$; Null Hypothesis that there should be no difference assumes similar numbers of each tree type were examined in each area, which is at least not very misleading). Hence this study implies that *B. perversa* is absent from the most severely polluted areas, that it occurs only on the most basic substrates (mortared walls and elder bark) in the most polluted areas that it can inhabit, and that it is less demanding with regard to the substrate in surrounding and otherwise fairly similar areas that suffer less pollution.

The greater effect of atmospheric pollution on the distribution of *B. perversa* than on that of *L. marginatus* might be associated with the apparently lower tolerance of acid substrates shown

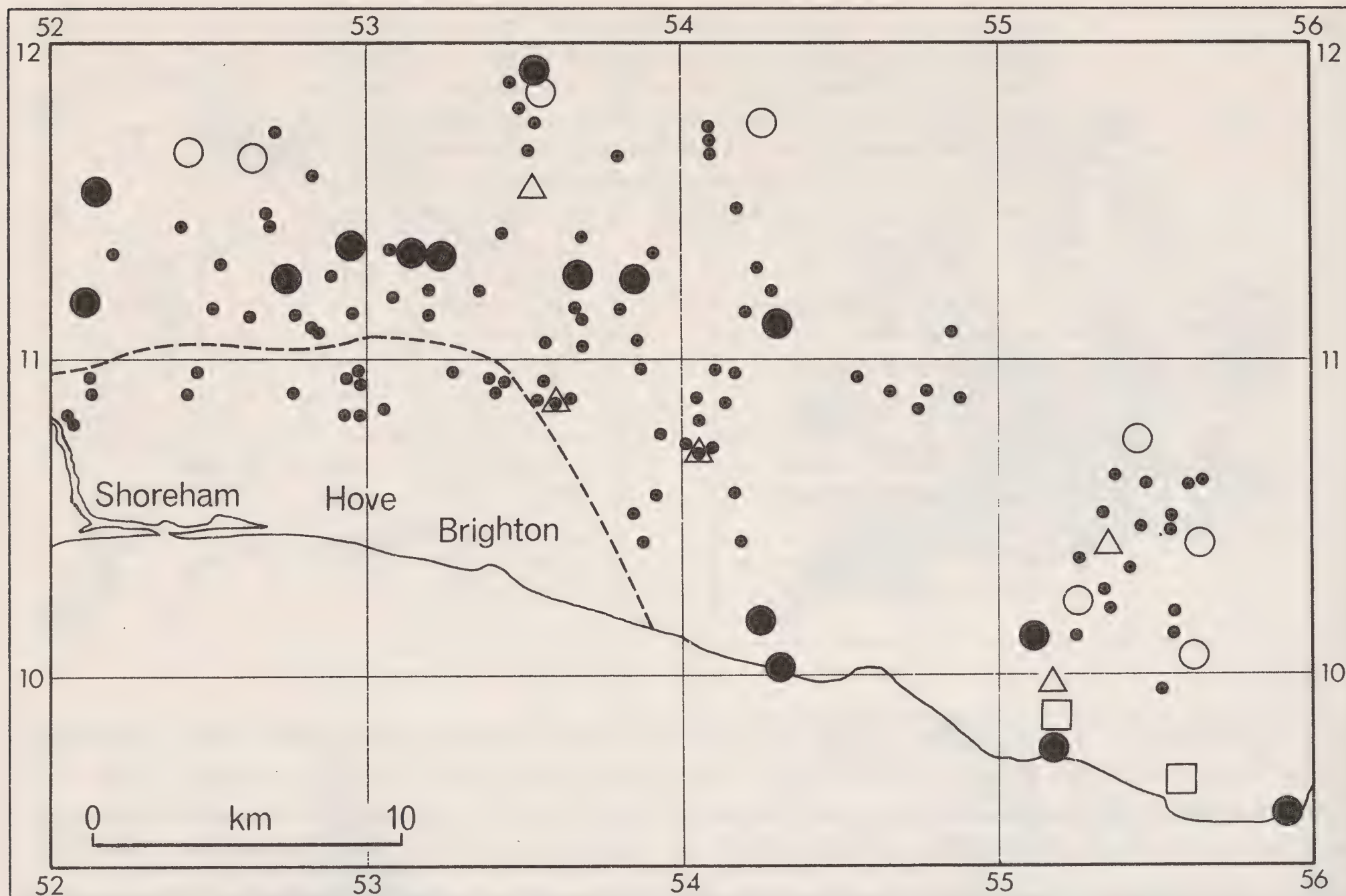


Fig. 2. Distribution of *Balea perversa* in part of Sussex, England. The numbered lines show the ten km squares of the National Grid. The pecked line encloses the area from which the pollution sensitive lichen *Parmelia perlata* is absent (fide Hawksworth and Rose 1976, Fig. 5-1). The large points all show localities at which *B. perversa* was found: closed circles, on elders; open circles, on elms; squares, on hawthorns; triangles, on walls; small closed circles show sites at which *B. perversa* could not be found on tree trunks (incomplete).

by *B. perversa*. However, there are doubtless many other ecological differences between these two species. It is possible that increasing acidity of tree bark following pollution has had a direct adverse effect on *B. perversa*, but controlled field experiments involving removal of lichen and alteration of the pH of tree bark are needed to separate effects of different and possibly interacting factors that could have contributed to this decrease.

ACKNOWLEDGEMENTS

I am grateful to Dr. P. Harvey for assistance and advice when he was supervising this study, which was carried out at the School of Biological Sciences, University of Sussex. I would also like to express my thanks to Dr. E. O. Bishop, Dr. B. Coles, Dr. M. P. Kerney and Dr. R. B. G. Williams for bringing records of *B. perversa* to my attention and for helpful discussion. Mr. H. Walkland helped in preparation of the figures. Special acknowledgement is due to the many members of the Conchological Society of Great Britain and Ireland whose careful field recording made much of this study possible.

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AFRICAN DISTRIBUTION OF GENERA AND SUBGENERA OF THE FAMILY VITRINIDAE (PULMONATA)

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(Read before the Society, 18 February 1978)

Abstract: Anatomical examination of a series of samples of Vitrinidae from Africa indicates that the Genera *Calidivitrina* and *Phenacolimax* (*Arabivitrina*) are known from Central and East Africa only above 2000 m, while *Phenacolimax* (*Oligolimax*) only occurs in Libya up to 1000 m. Material is not specifically determined due to the need for a complete revision of African Vitrinidae. A list of localities, including type localities for published species, is given with references and other published data.

Several years ago Dr. B. Verdcourt sent me Vitrinidae from Kenya, and S. P. Dance, at that time curator of molluscs at the British Museum (Natural History), those collected by the Cambridge Botanical Expedition to Ethiopia in 1957. The study of both collections was begun, but circumstances caused its interruption for a long time.

Anatomical examinations enabled the determination of genera and subgenera, but specific determinations, which would require a prior revision of all species of the region hitherto described, must be left to a future worker. All the material is now in the British Museum (Natural History) (BMNH). Through the kindness of the late Dr. Nils H. Odhner of the Naturhistoriska Riksmuseum, Stockholm (RM), I have been able to re-examine the voucher material of the publication of B. Hubendick 1953.

Genus *Calidivitrina* Pilsbry 1919

Pilsbry (1919, p. 281) published *Calidivitrina*, type species *Vitrina oleosa* von Martens 1895, as a subgenus of *Vitrina* Draparnaud 1801. He mentioned as characters distinguishing *Calidivitrina* from *Vitrina* s.s., the following: The shell has none of the punctation of the first whorl. The mantle has no shell-lobes, or if present, they are so small that they disappear by contraction in alcohol. The marginal teeth all have simple, thorn-like cusps, not bifid as some of them are in typical *Vitrina*.

The study of different species of *Calidivitrina* and *Vitrina* s.s. reveals that only the character of the marginal teeth is a constant difference between the two genera. The protoconch of *Vitrina angelicae angelicae* Beck 1837, from Greenland, differs from other species of typical *Vitrina* by the absence of microsculpture (Forcart 1955, pp. 161-2, pl. 12, fig. 7). The shell-lobes of the mantle vary in different species corresponding to the size of the shell, being small in species with well-developed shells and large in species with reduced shells. The marginal radular teeth of *Vitrina* s.s. differ from those of *Calidivitrina* not only in having bifid cusps, but also by the lateral serration below the ectocone (Pilsbry 1946, p. 500, fig. 274B).

Pilsbry did not mention any differences in the genitalia. As in all genera of Vitrinidae except *Vitrina* s.s., the spermatheca of *Calidivitrina* enters the vagina (Hubendick 1953, p. 88, figs. 21-23, schematic sections through the distal genitalia), but in the genus *Vitrina* it is inserted

between the vagina and the penis directly into the atrium (Forcart 1955, p. 161, figs. 1–5). The genitalia of the European *Eucobresia* Baker 1929, which have similar external morphology, differ by possessing an internal papilla interrupting the vagina (Forcart 1944, pp. 641–651, figs. 2, 4, 6), which is missing in *Calidivitrina*.

Distribution. Mt. Ruwenzori (= Runssoro) at the frontier between Uganda and Kivu Province, Zaire: type locality of *Vitrina oleosa* von Martens 1895, and *V. cagnii* Pollonera 1906. Von Martens (1897, p. 40, pl. 3, fig. 4) gives descriptions of the animal, shell, jaw and radula of *V. oleosa*. Pilsbry (1919, p. 284, figs. 17–18) classified *V. cagnii* as a junior synonym of *V. oleosa* and described the animal, shell, jaw, radula and genitalia. Hubendick (1953, p. 89, figs. 17–18) illustrated the genitalia under the name *V. oleosa* (RM No. 3117–3124).

Mt. Karisimbi, Kivu Province, Zaire, 1° 31'S, 29° 25'E: type locality of *Vitrina tenuissima* Thiele 1911. Hubendick (1953, p. 85, fig. 12, genitalia of paratype).

Mt. Elgon on the frontier between Kenya and Uganda: type locality of *Vitrina variopunctata* Connolly 1931. Hubendick (1953, pp. 87, 89, fig. 16, genitalia, as '*Vitrina* sp.'; RM No. 2528, 3125–3130).

Kipraos, near Timboroa, Uasin Gishu District, Kenya, 0° 04'N, 35° 33'E. Verdcourt coll. (BMNH).

Thompson's Falls, Kenya, 0° 04'N, 36° 22'E. Verdcourt coll. (BMNH).

Aberdare Range, Naivasha District, Kenya. Hubendick (1953, p. 85, figs. 5, 6, 23 genitalia, as '*Vitrina* sp.'; RM No. 3113–4); Verdcourt coll. (BMNH).

Katamayo, Kiamba District, Kenya. Verdcourt coll. (BMNH).

Mt. Kenya: type locality of *Vitrina lactea* Connolly 1925. Hubendick (1953, pp. 83–4, figs. 1–2, 21, genitalia, as '*V. lactea*'; and pp. 84–5, figs. 3–4, 22, genitalia, as '*V. baringoensis* Smith 1894'; RM No. 3115–6); Verdcourt coll. (BMNH). Verdcourt mentioned in lit. 'The "*V.*" *baringoensis* mentioned by Hubendick is definitely a mistake, I feel, since according to Connolly, Smith's type has microspiral striae on the apex as in *Helicarion*.'

Mt. Meru, Arusha Province, Tanzania. Hubendick (1953, p. 85, figs. 8–9, genitalia, as '*V. nigrocincta* von Martens'; RM No. 1194–1200).

Mt. Kilimanjaro, Kenya: type locality of *Vitrina nigrocincta* von Martens 1897, *Vitrina lobeliaecola* Dautzenberg 1908, *Vitrina ericinella* d'Ailly 1910, *Vitrina viridisplendens* d'Ailly 1910 and *Vitrina kiboschoensis* d'Ailly 1910. Hubendick (1953, pp. 85, 87, fig. 13, genitalia of paratype of *V. ericinella*; p. 87, fig. 14, genitalia of paratype of *V. viridisplendens*; and p. 87, fig. 15, genitalia of paratype of *V. kiboschoensis*; RM No. 1194–1226; 1584, holotype of *V. ericinella*; 1583, holotype of *V. viridisplendens*; and 1582, holotype of *V. kiboschoensis*).

Genus *Phenacolimax* Stabile 1859.

Forcart (1956, pp. 115–7) revised the systematics and taxonomy of the genus *Phenacolimax* and its subgenera. The genus is characterized by its erectile vaginal papilla, as described by Forcart (1949, figs. 1–2) and Hubendick (1953, p. 88, fig. 24).

Subgenus *Arabivitrina* Thiele 1931.

African distribution. Mt. Muhavura on the frontier between Rwanda and Kivu Province, Zaire, 1° 23'S, 29° 40'E. Hubendick (1953, pp. 89–90, figs. 19, 24, genitalia, as '*Vitrina* sp.').

Dalato, S. Ethiopia, 3000 m altitude? (Dodola 6° 59'N, 39° 11'E?). Hubendick (1953, p. 90, fig. 20, genitalia, as '*Vitrina neumanni* Thiele 1933').

Gojam Province, Ethiopia. Cambridge Botanical Expedition to Ethiopia, 1957 (BMNH).

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Subgenus *Oligolimax* Fischer 1878.

African distribution. Gharyan Mt., Tripolitania, Libya, 32° 12'N, 13° 02'E: type locality of *Vitrina tripolitana* Sturany 1909 and *Phenacolimax (Oligolimax) sturanyi sturanyi* Forcart 1959. Forcart (1959, p. 2, pl. 1, fig. 4, as '*P. (O.) tripolitana*'; pp. 2-3, pl. 1, fig. 2, as '*P. (O.) sturanyi sturanyi*').

Cyrenaica, Libya: type locality of *Phenacolimax (Oligolimax) sturanyi brandti* Forcart 1959 and *P. (O.) zilchi* Forcart 1959. Forcart (1959, pp. 3-4, fig. 1, genitalia, pl. 1, fig. 3, as '*P. (O.) sturanyi brandti*'; pp. 4-5, pl. 1, fig. 5, as '*P. (O.) zilchi*').

The genus *Calidivitrina* and the subgenus *Arabivitrina* are known in Africa only from highlands over 2000 m altitude, the subgenus *Oligolimax* only from Libya up to 1000 m. Only the distribution of the specimens examined and of type localities in the regions mentioned are cited.

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YOLDIELLA LUCIDA (LOVÉN 1846) (BIVALVIA) IN THE IRISH SEA

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(Read before the Society, 20 May 1978)

Abstract: The discovery is noted of a single valve of the rare British bivalve *Yoldiella lucida* in a sample of shell debris from Liverpool Bay.

In 1972 I was asked by the Institute of Geological Sciences (Yorkshire and East Midlands Unit), to look at some grab samples of shell debris, gathered from various parts of the Irish Sea during 1968. In one of these samples taken from the sea bed some sixty km south-east of Douglas, Isle of Man, and forty-five km west of Blackpool, (Lat. $53^{\circ}42.1' N$. Long. $3^{\circ}46.3' W$.), a single apparently fresh valve of the rare bivalve *Yoldiella lucida* (Lovén 1846) (= *Portlandia lucida* (Lovén)) was found.

Records of this species in British waters are few and confined to deep water off Ireland and northern Scotland (Jeffreys 1869: 173). Its occurrence, therefore, in the relatively shallow waters of Liverpool Bay is rather surprising. *Yoldiella lucida* is considered to be a northern arctic species and is known off the coasts of Denmark and Sweden at depths varying from 50 to 500 m but more commonly from 100 to 300 m (Soot-Ryen, personal communication). It is also known to occur off the coasts of North Carolina, Greenland and in the Mediterranean (Tebble 1966).

The possibility of the valve being a reworked Postglacial fossil has been considered, as it is known to occur commonly in deposits in Scandinavia, and a hypothesis has been put forward by Dr. P. E. P. Norton (personal communication) that the specimen might be from a cold marine phase of Late glacial or early Postglacial times. As far as I have been able to establish, however, none of the known deposits which extend under the Irish Sea has yet produced a record of this species.

The true status of this record may never be fully established, but as no other material in the samples was suspect, I feel justified in putting this record forward as of probable modern occurrence.

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THE EVOLUTION OF THE CONCHOLOGIST

P. E. NEGUS

(Presidential address, delivered 18 March 1978)

The prospect of a Presidential Address is always rather frightening, but, listening to other Presidents tackling the problem, I was encouraged by two things. Firstly, it can be as brief or as long as one wishes and, secondly, there is freedom of choice of subject with no questions to answer at the end. So I have chosen the Evolution of the Conchologist since I see no reason why we should not review our own relationship with the Mollusca from an evolutionary point of view, in much the same way as we would look at any other animal, vertebrate or invertebrate, in the natural environment. For example, Man's relationship with the dog has always been that of master; with the cat, that of an inferior (however unwillingly); with the reptiles, insects and arthropods, he has maintained a precarious and uneasy relationship, based on mutual suspicion! Obviously, comments on Man's earliest contact with the molluscs must be a matter of conjecture, although one can make reasonable guesses. At this point I would stress that I am not much concerned with dates in this context, but rather with a sequence of events and developments. It is likely that Man's earliest encounter with the molluscs was in the search for, and experimenting with, food, to augment the supply produced by hunting, some time during the Palaeolithic—a suitably long and vague time sequence. This would probably have been limited to comparatively few people who happened to wander near the sea shore, estuaries, etc. In the following period, the Mesolithic, Man tended to rely more on collecting food and less on hunting, in the strict sense of the word, and so it seems probable that it was then that Man really established the first thread in the pattern—the 'Can I eat it?' strand which has continued to the present time. Probably about the same time or soon after discovering that some shell-fish were good to eat, men were attracted by the colour and shape of some shells and gave them to their womenfolk for ornaments. This established the 'Can my girl-friend wear it?' thread, which runs through the pattern to today. And then there was the charm or amulet use of molluscs—'Will it bring me good luck or protect me from the Evil Eye?'. At quite an early stage too, the purely practical use of shells must have been appreciated—as containers, particularly for primitive oil lamps—either concave valves of bivalves or gastropods.

From these remote times of the Palaeolithic and Mesolithic, camp or temporary settlement sites which have been preserved are few, and it would be difficult to obtain any definite evidence. However, recent discoveries in well-stratified Palaeolithic deposits in a cave on the coast near Nauplion, southern Greece, have produced snails and shell-fish amongst seeds, nuts and wild grain. When we come to the *Neolithic*, a considerable amount of relevant material has come to light in recent decades, particularly in the Near and Middle East, which is of importance to my theme. For example, in Palestine, at Jericho, in the 8th millennium BC, human skulls were plastered over with a lime mud to mould the features and cowries and also bivalves were inserted in the eye sockets. These 'sculptured' skulls were found under the floors of dwellings, and were, presumably, revered ancestors. This use of molluscs at quite an early date, other than for purely practical purposes, indicates observation, imagination and trading to obtain the shells. As the millennia went by, more and more examples occur of shells as

ornaments (gastropods, scaphopods and bivalves) in graves in many countries. In Egypt shells as amulets, both the actual shells, perhaps inscribed or carved, and reproductions of shells in faience or other material were common. From Ur, in ancient Sumeria, comes an early oil lamp—a bivalve shell. Gradually shells began to influence art forms and decoration in the early Mediterranean civilizations; the Minoan culture of Crete being a prominent example. In the 2nd millennium BC, many vases were painted with gastropods (*Murex*), squids, octopuses, as well as many other marine subjects. From Zakro, in Eastern Crete, comes a faience model of an argonaut—‘paper nautilus’—found in recent years. After about 1000 BC a considerable ‘molluscan’ industry had developed at Tyre and Sidon in Phoenicia, and later at other places in the Mediterranean—the Tyrian purple, that much-prized dye obtained from a variety of species of gastropods and requiring huge quantities of shell-fish for the manufacturing processes. It is, perhaps, this particular use of molluscs which typifies the attitude of Man to the molluscs. That is, with few exceptions in the past, he has regarded them as a resource, just as much so as copper or gold deposits, or the Lebanon Cedars, or the skins and furs of animals.

Coming down to Greek and, later, Roman culture, the scallop—already used in the Bronze Age in the Cyclades—is really launched on its long career as a familiar motif—as a background for Aphrodite and other goddesses in terra-cotta or in mosaics through to the modern ‘Shell’ petrol symbol. The concave valve of a scallop is commonly used as a café ashtray in our own time. It is even used in Burlington House!

Then, there are the conch shells used as trumpets or semi-religious musical instruments and the cowries used as ‘money’ or trading tokens. Of course, a great many instances of the foregoing could be cited from different countries and periods, but I am well aware that several entertaining and well-informed talks have been given to the Society in recent years covering the influence of shells in arts and crafts, and the history of famous shell collectors and collections of the past and the expeditions to find rare shells. I have simply selected a few random cases to fill in the background to my theme to establish Man’s relationship with—and use of—the molluscs, and his attitude to the group.

Having reached the Greeks and Romans, we have some early recorded observations of various aspects of natural history, giving a slight insight into Man’s curiosity about his environment and neighbours. It is against this background that we must set the early days of the collector of curiosities. It is impossible to say when anyone started to collect shells for their own sake, that is, apart from having a specific use or application in view. In any case, the early days of natural history collecting were influenced by superstition and folklore, and a long process of refining and specialization was yet to come. At this point it is worth stressing that there may well have been individuals at different times who were curious and observed living molluscs without any ulterior or practical motive, but, inevitably, this is a matter of conjecture, although an important element in the evolution of the Conchologist.

The acquisitive instinct is strong in *Homo sapiens*, and it is probably around the 14th–15th centuries that well-to-do leisured people and scholars started to accumulate the heterogeneous collections of natural history, historical and ‘fantastical’ objects which formed these early ‘cabinets of curiosities’. Gradually it became a matter of pride for aristocratic families to boast such a collection, and the advent of printing stimulated the production of catalogues and descriptions of some of these ‘cabinets’ including references to shells, of course.

As the centuries went by, collectors tended to specialize rather more and to concentrate on mineral specimens or fossils, butterflies or shells and, as the various departments of natural history began to come into existence, a variety of books and essays were published, still often an amusing mixture of observed fact and flights of fancy.

Because of their very nature, shells tended to become divorced from their owners, the living animals, both as collectors’ ‘objects’ and as material for a natural history study, and this resulted in a certain dichotomy in Man’s attitude to the molluscs in the past, and it has been a slow process to bring the two parts together again.

Into the 18th and 19th centuries and shell collecting and molluscan studies increased in popularity, and so did the variety of publications—ranging from penny pamphlets to fine illustrated volumes and monographs. The influence of the molluscs on Literature—as distinct from the scientific or popular writing *about* molluscs—has been well demonstrated by A. E. Ellis with Poetry and Fables and by T. E. Crowley in the realm of Fiction. During this period, we know that there were individual naturalists who were faithful observers of molluscan life and some of them were obviously aware of the snail's place and part in a shared environment. However, to the great majority still, shells were taken for granted as were most natural resources, to be plundered and ransacked as convenient and expedient.

Inevitably, individuals of any species tend to evolve or adapt at different rates so that, at any given time, people's attitudes to our environment and the other species it contains, vary greatly.

It was during the middle and latter part of the 19th century that a number of natural history societies and clubs were founded to bring together those interested in the various departments—geology, conchology, mineralogy etc.—and to publish appropriate proceedings and journals, and so the conchologist has appeared on the scene as apart from, or in addition to, the general naturalist. It is bound to happen that individual workers unconsciously reflect something of the age in which they live and work and so, in the Victorian period, there is a noticeable tendency towards a more individual and 'personal' approach, with far less emphasis on team work and co-operative efforts than is the case today. The production and publication of the 'Atlas of Non-Marine Mollusca' during the Centenary Year of this Society, is an excellent example of the co-operation of many individuals making a contribution to a large-scale project. The various molluscan volumes in the Treatise on Invertebrate Palaeontology form another example of many people contributing to one important work. It is significant that people in the 19th and early 20th centuries often worked in comparative isolation and controversy and rivalry for prior publication of their works and personal 'battles' were a frequent feature.

Colonial expansion and increased exploration produced more shells for the collectors, the museums and the naturalists. But there was little thought of conservation in that period, when World population was at a relatively manageable level with high infant mortality and shorter lives, and there was far less pressure on habitats than is the case today.

I have purposely avoided a definition of the term 'conchologist' since this would imply a fixed attitude at a certain point of time, whereas my theme is the change and adaptation of that very attitude. The rapidly increasing pace and tempo in the 20th century has had a real and drastic effect on the molluscs and on Man's relationship with them. In the first two or three decades of this century there probably seemed to be little change in the overall pattern including the snails and the conchologist. But, gradually, there developed an increasing awareness of the pressures on the natural environment resulting from increasing population, industrialization and exploitation. And so, enlightened conchologists realized the urgent need to record as fully as possible—(consider here the Non-Marine and Marine Recording Schemes of this Society)—and to arm themselves with the information so necessary in publicizing and presenting cases for protection of habitats, removal of endangered colonies to safer sites, applying for legal protection of threatened species and for restricting collecting where necessary. This last factor brings me to a potentially controversial aspect of the evolution of the conchologist. It is implicit in Man's nature to want to collect beautiful and unusual natural objects, as is demonstrated in the history of our species, and it must be remembered that we are very much dependent on the great national collections accumulated during past centuries, forming an essential source of reference, research, information and entertainment. Whilst it is obviously necessary to collect material for study and publication, the unrestrained collecting of living things is bound to affect the very survival of some species and genera. The problem lies, as with so many of Man's activities, in maintaining a balance and introducing a form of discipline, either as a personal sense of responsibility or as state control, depending on the political system under which we happen to live. For example, the unlimited and uncontrolled collecting of

certain species of molluscs and corals for the fancy goods and souvenir trade can never be justified, either on ethical grounds or simply business common-sense—another example of proceeding to kill the goose that lays the golden cowry. There are, of course, plenty of instances in Man's history of the destruction of whole populations and species for a merely trivial or frivolous purpose, often dictated by fashions—the molluscs are no exception here!

At this point, I must admit that an early 19th century naturalist would probably consider that I have wandered far from my appointed path in touching on social and political attitudes and responsibilities. But the very stuff of evolution is change and adaptation; what may appear appropriate in one age may seem indefensible in another, and if our view of the Mollusca is too limited and 'blinkered', we may find that in ignoring and failing to conserve something of our general natural environment, we shall ultimately lose many of the very things which we set out to study and enjoy.

So, where is this idiosyncratic nature ramble of mine leading us? What conclusions can I draw? The important message is that we inherit from the past—both natural and man-made—we observe, record, interpret and conserve in order to hand on to future generations. In other words, we *must* see ourselves as caretakers or leaseholders of our natural environment, *never* as freeholders or owners. I believe this is a vital distinction which could have a significant influence on our attitude to the problems facing not only conchologists but all naturalists in the coming decades.

After all, a study of any branch of natural science should have taught us by now that, whether you are a coral polyp, a golden cowry or a human being, your success as a species depends ultimately on maintaining a balance between the individual, the group (colony or population) and the surrounding environment.

A PROPOSED NEW LIST OF
BRITISH ASCOGLOSSA
(OPISTHOBRANCHIA)

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(Read before the Society, 22 April 1978)

Abstract: The essential features of the new list are: the restriction of the family Hermaeidae to diaulic species; the restoration of the genera *Calliopaea* and *Placida*; and the transference of *Limapontia* to the family Stiligeridae. Ascoglossa is preferred as the name of the order. The list is based on a recent classification of the Ascoglossa by Baba and Hamatani (1970), modified by Gascoigne (1976).

It is right and proper that classifications should change and this is especially true of the order Ascoglossa (= Sacoglossa) in which the number of known species has almost doubled within the last fifty years. The discovery of bivalved gastropods required the addition of a suborder. Anatomical studies of some species, for example *Limapontia cocksi* and *Hermaea variopicta*, have resulted in the suppression of genera and the transference of species to different taxa. Many new species have been inadequately described and some may turn out to be subspecies, or less. Thus changes are necessary, if we are to have a sound and logical order.

The lists of Winckworth and of Thompson illustrate the changes that have been made in the classification of the British Ascoglossa. Winckworth's arrangement (1932, 1951), shorn of its taxonomical trimmings, is as follows:

Order Ascoglossa

Family	Stiligeridae	
Genus	<i>Hermaea</i> .	<i>H. bifida</i> ; <i>H. dendritica</i> .
	<i>Stiliger</i> .	<i>S. bellulus</i> .
	<i>Alderia</i> .	<i>A. modesta</i> .
	Elysiidae.	
	<i>Elysia</i> .	<i>E. viridis</i> .
	Limapontiidae.	
	<i>Acteonia</i> .	<i>A. senestra</i> .
	<i>Limapontia</i> .	<i>L. capitata</i> , <i>L. depressa</i> .

In his *Biology of opisthobranch molluscs*, Vol. 1 1976, Thompson brought Winckworth's list up-to-date, and modified his classification; these changes are shown in the following outline:

Order Sacoglossa
suborder Elysiacea

Family	Stiligeridae	
Genus	<i>Hermaea</i> .	<i>H. (Hermaea) bifida</i> , <i>H. (Hermaea) variopicta</i> , <i>H. (Placida) dendritica</i> .
	<i>Alderia</i> .	<i>A. modesta</i> .
	<i>Stiliger</i> .	<i>S. bellulus</i> .
	Elysiidae	
	<i>Elysia</i> .	<i>E. viridis</i> .
	Limapontiidae.	
	<i>Limapontia</i> .	<i>L. capitata</i> , <i>L. depressa</i> , <i>L. senestra</i> .

A third list is now proposed in which a new classification is used—that of Baba and Hamatani (1970), modified by Gascoigne (1976). Some brief remarks are appended.

Order Ascoglossa

Family	Elysiidae	
	Genus <i>Elysia</i>	<i>E. viridis</i>
	Hermaeidae	
	<i>Hermaea</i>	<i>H. bifida</i> , <i>H. variopicta</i>
	Stiligeridae	
	<i>Calliopaea</i> .	<i>C. bellula</i> , <i>C. oophaga</i> (?)
	<i>Placida</i> .	<i>P. dendritica</i> .
	<i>Limapontia</i> .	<i>L. capitata</i> , <i>L. cocksi</i> , <i>L. depressa</i> .
	Alderiidae	
	<i>Alderia</i> .	<i>A. modesta</i> .

In 1875 Pagenstecher named the order Monostichoglossa, and a year later it was simultaneously renamed Sacoglossa by Ihering and Ascoglossa by Bergh (Ihering, 1876). Since then the cumbersome name Monostichoglossa has fallen into disuse, and nowadays some zoologists use Sacoglossa, others prefer Ascoglossa. In England, for example, the name Sacoglossa is now fashionable, whilst authors in America, Australia, and Japan, favour Ascoglossa. The question arises which of the two names is the better? The present choice is made for reasons given below, for although the *International Code of Zoological Nomenclature*, 1964, does not give rules for taxa above family rank, its principles and recommendations provide a guide to rational conduct at higher levels. For example, Appendix D2, 11 of the Code recommends that in forming a compound name a zoologist should not choose components one of which is Latin and the other Greek. Now the first part of Sacoglossa is Latin (from *saccus*, a sac; misspelt in the component as Saco-) and the other part is Greek; whereas both parts of Ascoglossa are Greek. It would be more in accordance with classical learning to prefer Ascoglossa. A sound practical reason for not using Sacoglossa is that its spelling comes too close to that of *Saccoglossus*, a genus of the Hemichordata; this is supported by a recommendation of the Code (D, 5b).

Both Ascoglossa and Sacoglossa refer to Alder and Hancock's false conception that the radula functioned as a tongue. More suitable names would be Saccodentia and Ascodontia, for they indicate that the hallmark of the order is a sac containing teeth. But I would not seriously propose either of these two names because Ascoglossa has been in use for over a hundred years; in other words, I am guided by the principle of priority as set out in the preamble to the Code.

In the 1930's it was generally held that *Elysia viridis* was the typical sacoglossan and that the family Elysiidae occupied a central position in the superfamily Elysiacea; these opinions are no longer held by many specialists. The sequence of families in the third list reflects the close relationship between Hermaeidae and Stiligeridae and this is discussed in a paper by Gascoigne (1978, in the press). The two families are also similarly placed in a checklist by Marcus (1977).

The trouble with the order Ascoglossa is that most of its species are small, some of them look alike, and, being soft and slimy, their internal anatomy is difficult to determine, especially the complicated reproductive system. The result has been that zoologists were sometimes at a loss when grouping new species. At first *Hermaea* was fashionable and Bergh (1878) enlarged the genus by including *Hermaeina*, *Placida*, and *Hermaeopsis* as subgenera. At the beginning of the 20th century it was the turn of *Stiliger*. Baba has done most of the spade-work in clearing the resulting confusion by restoring and regrouping original genera, for example, *Calliopaea* and *Placida*.

After reading a draft of my paper, Baba suggested that the genus *Hermaea* (s.s.) could be maintained as the proper type of a restricted family Hermaeidae. One of its distinguishing features is the diaulic nature of the reproductive system: in contrast, stiligerids are triaulic or pseudo-diaulic. *H. bifida* and *H. dendritica* differ so markedly in their reproductive systems that this cannot adequately be expressed in terms of subgenera (Gascoigne, 1976); consequently *H. dendritica* is transferred to the genus *Placida*, because it shows some resemblance to the type species, *P. viridis*, in its central nervous system, gut, and reproductive system (paper in preparation).

Eliot (1910) transferred *Calliopaea bellula* to the genus *Stiliger* on insufficient anatomical evidence. Recent studies by Gascoigne and Todd (1977), and Gascoigne and Sigurdsson (1977) show that the differences between *Stiliger* and *Calliopaea* are enough to maintain them as separate genera.

Limapontiids differ greatly from other ascoglossans in external features. However, they possess most of the internal characteristics of the Stiligeridae, including a nervous system with only two ganglia on the visceral loop, and a stiligerid reproductive system. The evidence of internal anatomy outweighs that of the external features and so the genus *Limapontia* appears in the family Stiligeridae. The Law of Priority would require a family-group name erected in 1923 (e.g. Stiligeridae, Iredale and O'Donoghue) to yield to one erected in 1862 (e.g. Limapontiidae, Hancock). However, Limapontiidae has been used only in a restricted sense (since Gascoigne, 1973, for *Limapontia* only) whereas Stiligeridae has been used for an ill-defined group of genera. This arrangement seems to me to reflect the current state of taxonomic knowledge better than one which would imply a spurious degree of certainty—as would be so if the Law of Priority were strictly followed. The case will be presented to the Commission for consideration.

Concerning the name *Limapontia cocksi*, I was admittedly wrong in my 1973 paper to depend on Art. 1 of the Code, since Quatrefages (1844) did not describe *Acetonia senestra* as a teratological specimen. However, since I am convinced that it was a teratological specimen, I cannot regard its name as anything but a *nomen dubium*. That is my true reason for rejecting it; therefore the name *L. cocksi* is maintained.

The question mark placed after *Calliopaea oophaga* indicates there is some doubt about its status. It may be a subspecies of *C. bellula*, but it cannot be a synonym of *Stiliger vesiculosus* (Deshayes), since this species differs distinctly from *C. bellula* and *C. oophaga* in its teeth and penial style. *Alderia modesta* has no heart, its gut is distinctive, and, although it has a penial style and is pseudo-diaulic, its reproductive system is not of the stiligerid pattern. For these reasons *Alderia* is placed in the family Alderiidae.

A regional checklist, like that proposed for the British Isles, should be brought into line with a world list. Baba kindly sent me his world list of ascoglossan species which I hope will soon be published; the arrangement used in the new list of British species agrees closely with that of Baba's world list. It is true that the changes proposed in the British list have been previously mentioned in papers by Gascoigne. They are here brought together in a convenient form, so that they may be considered by the Conchological Society before Winckworth's authoritative list is revised.

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AN EVALUATION OF THE
NOTASPIDEAN GENERA
PLEUROBRANCHOPSIS VERRILL
AND *GYMNOTOPLAX* PILSBRY
(OPISTHOBRANCHIA:
PLEUROBRANCHINAE)

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(Read before the Society, 20 May 1978)

Abstract: This paper presents a clarification of the status of two pleurobranch genera that have repeatedly been misunderstood and caused confusion. Since the holotype of *Pleurobranchopsis aurantiaca* Verrill 1900 (= *Pleurobranchus verrilli* Thiele 1931) is apparently lost, there can be no certainty about its taxonomic position and the taxon should be treated as a *nomen dubium*. Examination of the holotype of *Pleurobranchus americanus* Verrill 1885 (type species of *Gymnotoplax* Pilsbry 1896) shows it to be a species of *Berthella* Blainville with the mantle mutilated to such a degree that the shell has been uncovered. It is doubted that any members of the Pleurobranchidae exist in the living state with partially or wholly uncovered shells.

This publication is the second of a series in which the author is attempting to assess the taxonomic status of proposed genera within the opisthobranch order Notaspidea. In this study I am reviewing some of the rather numerous genera and grouping them so as to establish proper synonymies within the framework of the current understanding of the systematics of the order (Odhner 1926, Burn 1962). Results are given here for *Pleurobranchopsis* Verrill 1900 and *Gymnotoplax* Pilsbry 1896, both genera within the subfamily Pleurobranchinae, whilst an earlier paper dealt with the Pleurobranchaeinae (Willan 1977).

Pleurobranchopsis and *Gymnotoplax* are both based on single specimens described by Addison Emory Verrill (1839-1927), who from 1864 to 1907, was Professor of Zoology at Yale University. Therefore, since these genera are both traceable to the works of Verrill, it is appropriate to treat them in one paper. A second point shared by both genera is the confused interpretations subsequent workers have put on them, indeed this study was precipitated by Abbott's (1974) use of *Gymnotoplax* as a substitute for the established taxon *Berthellina* Gardiner. These varying interpretations are understandable in view of the insufficient original descriptions and subsequent failure of workers to recheck holotypes where they are still in existence. Although the two genera are included in this paper, I shall treat them separately because their histories are quite different.

GENUS *PLEUROBRANCHOPSIS* VERRILL 1900

Pleurobranchopsis Verrill 1900: 547.

Type species by monotypy *Pleurobranchopsis aurantiaca* Verrill 1900 (= *Pleurobranchus verrilli* Thiele 1931).

History. Verrill (1900) described a single specimen taken at low tide from Cloney Island, Bermuda. This specimen was figured on Plate 66, Fig. 5. Verrill gave a brief description of the external appearance, colour and an egg mass which he supposed to belong to *Pleurobranchopsis aurantiaca*. He differentiated *Pleurobranchopsis* from *Pleurobranchus* Cuvier (shell lacking and sessile gill in the former) and from *Pleurobranchaea* Meckel in Leue (gill structure and free anterior mantle margin of the former). Thiele (1931) placed *Pleurobranchopsis* as a subgenus of *Pleurobranchus*, differentiating the former on the same characters of shell and gill that Verrill had used. This generic transfer made Verrill's name *aurantiaca* homonymous with *Pleurobranchus aurantiacus* Risso 1818 from the Mediterranean Sea, so Thiele renamed the species *Pleurobranchus (Pleurobranchopsis) verrilli*. Mattox (1953) and Abbott (1974) followed Thiele. Franc (1968) maintained *Pleurobranchopsis* as a full genus with the sole distinction of 'shell rudimentary or absent'. Thompson (1977) suggests Verrill had mischievous intentions when he introduced *Pleurobranchopsis aurantiaca*. It is significant that *Pleurobranchopsis* was omitted in both the major systematic summaries of the Pleurobranchidae that have appeared this century (Odhner 1926, Burn 1962).

As the original description was clearly inadequate, I wrote to Dr. R. T. Abbott enquiring as to the location of the holotype of *Pleurobranchopsis aurantiaca* (and incidentally that of *Pleurobranchus americanus* Verrill as well, see later). Dr. Abbott replied that Verrill's types are deposited both at the Smithsonian Institution, National Museum of Natural History, Washington and Peabody Museum of Natural History, Connecticut (personal communication March 1977).

Dr. Rosewater of the former institution looked thoroughly through their collections but there was no sign of *P. aurantiaca* (personal communication April 1977). Professor Hartman of Yale University informed me that all of Verrill's Bermuda material should have been deposited at the Peabody Museum, but the holotype could not be located there either (personal communication April 1977). Therefore the holotype of *Pleurobranchopsis aurantiaca* Verrill must be assumed to be lost.

Discussion. Since *aurantiaca* Verrill had been rejected as a secondary homonym of *Pleurobranchus aurantiacus* Risso prior to 1961, it must remain invalid (Bulletin of Zoological Nomenclature 31(2), 1974. Art. 59b(i)). From the inadequate original description it is not possible to determine with certainty whether *Pleurobranchopsis* is a synonym of *Pleurobranchus* Cuvier, *Berthella* Blainville or *Berthellina* Gardiner. The chief character used to distinguish the genus (absence of a shell) would now not be weighted so heavily. When Verrill says in the diagnosis of the genus 'shell absent' and 'no shell', it is not clear whether he actually opened the mantle and could find no shell or whether there was no shell visible externally (i.e. able to be delineated through the translucent overlying mantle) in his specimen. In *Berthellina* there is a reduced internal shell, but this is often invisible in both live and preserved specimens and the mantle must be cut open to expose it. It is also true however, that specimens of normally shelled *Berthellina* species can be found without a shell (e.g. Edmunds and Thompson 1972).

The second character to which Verrill gave importance 'gill attached along its entire length, or nearly so' is very hard to gauge in pleurobranchs. Much more important characters of greater assistance would have been the nature of gill rachis and site of the anal opening above the gill, but Verrill did not record these.

The relatively small size, smooth mantle and coloration described by Verrill could be attributes of either *Berthella* or *Berthellina*. As far as coloration is concerned, the description of *Pleurobranchus amarillius* Mattox, with type locality from Isla de la Gata, Parguera, Puerto Rico is quite similar to that described by Verrill (this species is considered by Burn (1962) and Marcus and Hughes (1974) to be a probable synonym of *Berthellina quadridens* (Mörch)). Mattox's description (1953: 110) reads: 'The colour of the living animal, young and adults, is a uniform bright yellowish orange.'

On the other hand the mantle of *Pleurobranchus atlanticus* Abbott (type locality, Biscayne Bay,

Florida) is 'yellowish orange with irregular splotches of deep maroon-brown . . .' and the foot is 'a translucent pale yellowish orange' (Abbott, 1949). Since *P. atlanticus* is now considered a synonym of *Pleurobranchus areolatus* Mörch (Marcus and Marcus 1967, Bertsch and Smith 1973, Abbott 1974), Dr. Abbott suspects *verilli* Thiele is *areolatus* Mörch (personal communication April 1977) thus making *Pleurobranchopsis* a synonym of *Pleurobranchus*. My feeling is that it is impossible to decide with certainty on the generic position of *Pleurobranchopsis* since there is no information existing on crucial taxonomic characters, such as details of radula, jaws and reproductive system internally or gill details externally.

With the knowledge that the holotype is probably lost, the sketchiness of the original description and doubt as to generic placement, it is advisable to treat the combination *Pleurobranchopsis aurantiaca* Verrill (= *Pleurobranchus verilli* Thiele) as a *nomen dubium*. Thus the genus is omitted from systematic considerations within the Pleurobranchidae until such time as the holotype is rediscovered and adequately described.

GENUS *GYMNOTOPLAX* PILSBRY 1896

Gymnotoplax Pilsbry 1896: 210.

Type species here designated, *Pleurobranchus americanus* Verrill 1885.

History. The description of *Pleurobranchus americanus* was based on a single specimen which had been dredged off the New England coast (475 m., off Martha's Vineyard, Massachusetts). The description was made after the specimen had been preserved in alcohol. Verrill gave a figure of *Pleurobranchus americanus* which has been reproduced twice (Pilsbry 1896, Abbott 1974).

Pilsbry (1896) created *Gymnotoplax* with the following brief description: 'Similar, so far as known, to *Pleurobranchus*, but the mantle is partly open or perforate above, exposing part of the shell. This condition occurs in no other Pleurobranchidae'. He repeated Verrill's description *verbatim* and included a second species, *Gymnotoplax martensi* Pilsbry (= *Pleurobranchus scutatus* von Martens in Möbius 1880, non *P. scutatus* Forbes 1844) which could be distinguished by 'the deep anterior cleft in the mantle'. Since Pilsbry did not give a type species for *Gymnotoplax* in 1896 and none has apparently been subsequently designated, the first species treated by Pilsbry (*Pleurobranchus americanus* Verrill) is here designated as type-species of *Gymnotoplax*. This choice is made not only because the diagnostic characters of Pilsbry's genus unquestionably belong to this species, but also the second species treated under *Gymnotoplax* by Pilsbry has subsequently been shown not to possess an uncovered shell as exhibited by *P. americanus* (Vayssi re 1898). In addition, there is a further argument against the choice of *G. martensi*, and that is that some recent workers are dubious about the identity of this species since no additional material has appeared since the original three (apparently damaged) specimens (Marcus 1977).

Bergh (1897) placed *Pleurobranchus americanus* in the synonymy of *Pleurobranchus aurantiacus* Risso, explaining (p. 120, footnote 2) that he had done this because of the size of the shell, as depicted in Verrill's original illustration. Vayssi re (1898, p. 357) doubted not only the placement of *Pleurobranchus americanus* in that genus, but even within the Pleurobranchidae and from Pilsbry's figure Vayssi re suggested *P. americanus* could be a cephalaspidean. Accordingly he did not recognize *Gymnotoplax*. Subsequently Vayssi re (1901, p. 74) suggested that the perforation could have been an accident resulting from a tear in the mantle. Odhner (1926) felt *Gymnotoplax* was probably identical to *Bouvieria* Vayssi re (a junior synonym of *Berthella*), and that the character of an incomplete mantle over the shell was of accidental occurrence in the typespecimen. Thiele (1931) treated *Gymnotoplax* as a separate genus defined by its large shell, and mantle which covered the shell only around the edges. Odhner (1939) referred to the genus in a search for an earlier name for *Berthellina* Gardiner 1936, he suggested *Gymnotoplax* could be a synonym of *Berthella* Blainville and added that the holotype of *Pleurobranchus americanus* was imperfectly known. Abbott (1949) felt *Gymnotoplax* to be sufficiently well characterized to be recognizable, but Pruvot-Fol (1954) was of the opinion that *Gymnotoplax* had been based on a mutilated

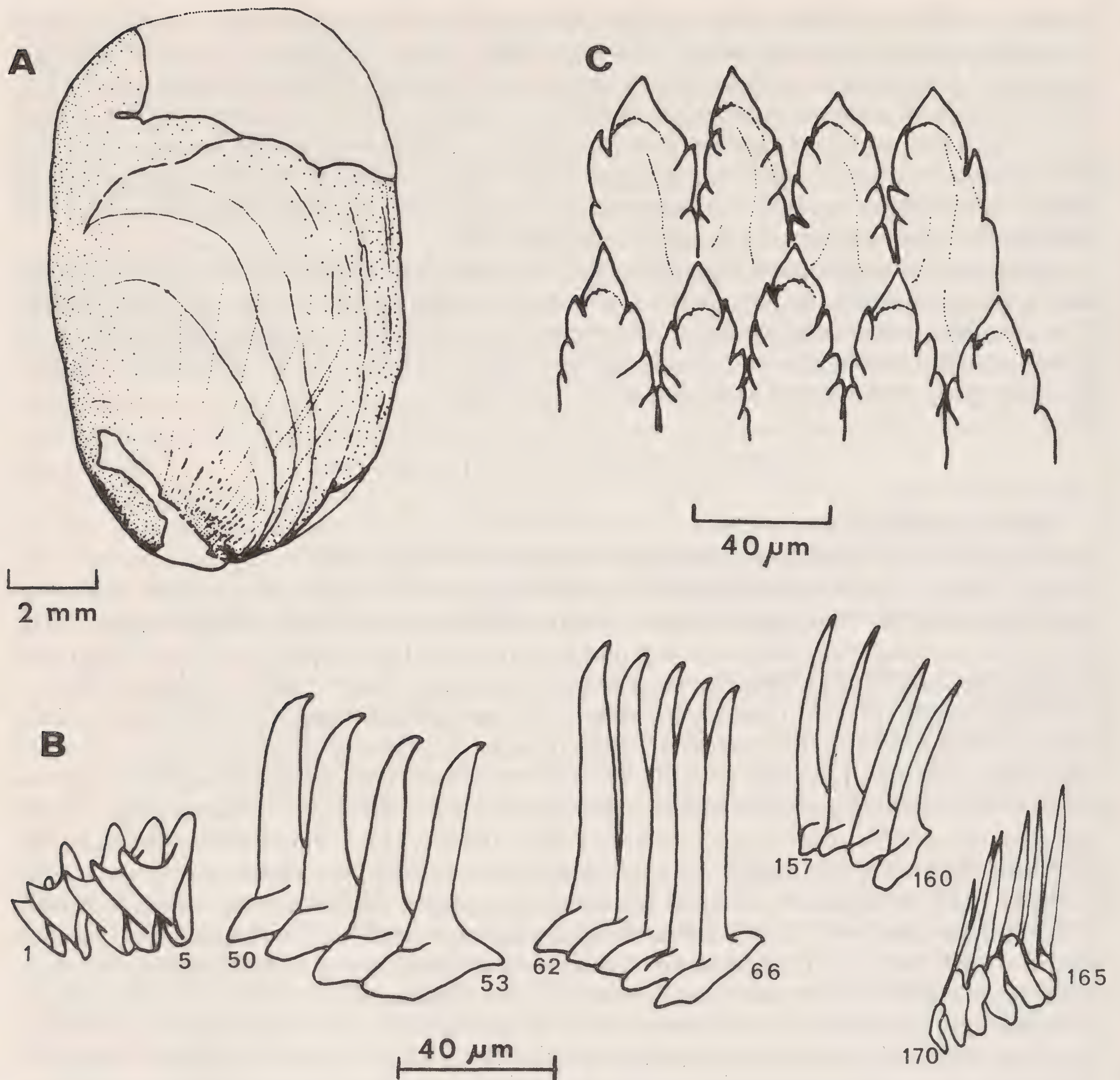


Fig. 1. Holotype of *Pleurobranchus americanus* Verrill; A, shell (partially reconstructed); B, radula; C, mandibular elements from inner face of jaw.

specimen in which the shell was not covered by the mantle. Franc (1968) followed Thiele (1931). Abbott (1974) overrode Odhner and treated *Berthellina* as a synonym of *Gymnotoplax*, thus attributing the well-defined characters of *Berthellina* to *Gymnotoplax*, and including four species. Bertsch (1975a) criticized Abbott's use of *Gymnotoplax*, noting that three of the species included by Abbott did not possess uncovered shells and thus could not be congeners of *Gymnotoplax americanus*. Marcus (1977) described a new species of pleurobranch from the Mediterranean Sea as *Gymnotoplax barashi*. Bouchet (1977) observed that following preservation, specimens of *Berthella sideralis* Lovén took on exactly the same facies as that originally illustrated for *Pleurobranchus americanus* by Verrill.

Because of the wide variety of opinions about *Gymnotoplax*, it became crucial to examine the

type specimen. Fortunately the holotype of *Pleurobranchus americanus* is still in existence, and is in the Smithsonian Institution under the registered number USNM 40,503. Dr. Rosewater kindly sent me the specimen and gave permission to dissect it. The following description summarizes observations that were made on the holotype.

Redescription of Holotype. Dimensions of body: length 13.4 mm; width 7.9 mm; height 6.4 mm. Dimensions of shell: length 12.6 mm; width 7.7 mm. Shell now incomplete, large, nearly covering the entire body, rather concave, auriculate, oval in shape with a low spire situated to the rear quite close to the middle of the shell, concentric growth lines prominent, under high magnification the shell surface is seen to have a microsculpture of closely-packed and regular punctations especially noticeable near the apex. Shell white, still faintly lustrous. Fig. 1A was reconstructed from the broken shell.

Whole body dull brownish colour, mantle edges thin, delicate and ragged where they have been torn and parted from the shell, but still the mantle is obviously very porous. No pedal gland discernable, oral veil simple, its anterior border is neither conspicuously sinuous nor postulose.

Gill on right hand side, rather elongate, attached for two thirds of its length, with the genital swelling and aperture just in front of, and below gill, reproductive organs not everted, gill rachis smooth, pinnae alternate, bipectinate, 24 pinnae counted on ventral side, 23 dorsally. Anal opening in front of middle of attached portion of gill, adjacent to the tips of fifth to seventh dorsal pinnae, total gill length 5.7 mm, and anus opens at 2.3 mm down its length.

A ventral incision was made through the anterior region of the foot of the holotype and the buccal mass removed. The reproductive organs were not dissected because this process would have completely shattered the exceedingly brittle shell.

Radula (Fig. 1B) with formula $85 \times 170.0.170$ (2 rows unthickened), counts of teeth across tenth and 60th rows showed the numbers of teeth per row to be nearly the same down the whole length of the radula. All the teeth are small, tightly-packed and simple in shape, innermost laterals broad-based, low, triangular and curved towards the growing end of radula (height 8–10 μm), teeth increase in size across the rows and towards the middle are larger (height 80 μm) with a very slight bend towards the tip, laterals decrease in size out from the middle (height 60 μm), outer lateral teeth slender and erect (height of outermost laterals 40 μm).

Jaws composed of rows of small interlocking mandibular elements (Fig. 1C). These elements are cruciform, exposed blades are tall (height of elements from apex of one row to apex of next row 40–50 μm) and denticulate laterally with 3 or 4 denticles on either side of a thickened terminal cusp.

Discussion. That *Gymnotoplax* is a synonym of *Berthella* Blainville was correctly anticipated by Odhner (1926, 1939) and Bouchet (1977). Vayssi re (1901) and Pruvot-Fol (1954) too, were right in believing the holotype to have been a mutilated specimen. The porous nature of remaining vestiges of mantle, shell, oral tentacles, rhinophores, gill, radula and jaws are all typical of *Berthella* and not of *Berthellina* Gardiner. Abbott (1974) had not examined this holotype (personal communication March 1977).

From my own experience with material of the Pleurobranchidae, in passing from the living state through the narcotizing process to fixation and preservation, it is possible to witness, on occasions, the mantle parting dorsally over the shell quite rapidly after death. I have noted this twice, with specimens of juvenile *Pleurobranchus forskali* R uppell and Leuckart and *Berthella postrema* Burn. After death there is rapid histolysis of the rather thin tissue of the mantle in the area immediately above the shell and the mantle disintegrates and tears open to expose the shell dorsally. Odhner (1926, p. 21) had verified this same transformation in his studies on *Bouvieria* (= *Berthella*). This change is enhanced in species that have especially thin (e.g. juvenile specimens) or porous mantles (e.g. specimens of *Berthella*). In my opinion this transformation has happened to the holotype of *Pleurobranchus americanus*, i.e. the mantle has become torn or

disintegrated after death (or in the dredge haul) to reveal the underlying shell. Some species of *Berthella* are also able to autotomize parts of their mantle (Sphon 1972).

Berthella americana can be briefly compared with the three other *Berthella* species of North America. On the East Coast is only *Berthella tupala* Marcus 1957, but in that species the radula is quite different (Marcus and Marcus 1967, Bertsch 1975b). On the West Coast are *Berthella sideralis* (Lovén 1847) and *B. kaniae* Sphon 1972. The latter is distinct and only the former resembles *B. americana*. *B. sideralis* has been taken only once, in Alaskan waters, by Dall in 1881. Judging from descriptions of *B. sideralis* given by Odhner (1939) and MacFarland (1966), it is quite close to *B. americana*. They both have large radular formulae and similar teeth, similar shells and microsculpture, but the denticles on the mandibular elements are coarser in *B. americana*. According to Odhner (1939) the anus of *B. sideralis* opens in front of the middle length of the gill membrane as is the case in *B. americana*.

The recognition that *Gymnotoplax* is a synonym of *Berthella* Blainville makes it necessary to revise the generic placement of species previously named as new within the former genus by Pilsbry (1896) and Marcus (1977) (*G. martensi* and *G. barashi* respectively). Vayssière (1898) re-examined the three specimens of *G. martensi* in Möbius' 1874 collection and augmented the original description given by Pilsbry (1896). He found spicules embedded in the mantle, denticulate blades to the mandibular elements and simple radular teeth with a radular formula of $70-80 \times 100.0.100$ but gave no mention of the gill structure (smooth or tuberculate). It would appear that *G. martensi* is either a species of *Berthella* or based on juveniles of a species of *Pleurobranchus*. As noted earlier, Marcus (1977) considers *G. martensi* a dubious species.

In my opinion, *Gymnotoplax barashi* Marcus 1977 is not congeneric with *Berthella americana* because of the tuberculate gill rachis, shell, radula and jaws of *G. barashi*. Six reasons lead me to suspect *G. barashi* is founded on damaged specimens of *Pleurobranchus* (*Oscanius*) *membranaceus* (Montagu 1815) and it is pleasing that the description of *G. barashi* by Dr. Marcus is sufficiently ample in its particulars to be able to reach this conclusion with confidence. Firstly, the tuberculate gill rachis is a character of the Pleurobranchinae (*sensu* Burn 1962). It does not occur in *Berthella* or other genera of the Berthellinae. The shell is large and nearly circular with the apex situated mid-posteriorly and is very similar to the figures of the shell of *P. membranaceus* given by Thompson and Slinn (1959) and Thompson (1976). The irregularly denticulate mandibular elements are also typical of *P. membranaceus* (Vayssière 1898, Pl. 25, Fig. 172). *P. membranaceus* is already known from the Mediterranean Sea (Thompson 1976). The final two reasons are even more compelling than these first four. In both specimens of *G. barashi* the penis is surrounded by 'an everted atrium which is continued into three lappets'. This is the non-retractile external sheath described by Thompson (1976) and is a well-known feature of the reproductive system of *P. membranaceus*. Vayssière (1898, p. 380) said: 'penis très long et très grêle, cylindrique, légèrement renflé à son extrémité, rétractile dans une gaine formée par un prolongement charnu en forme de tronc de cône, de la base duquel partent trois expansions membraneuses triangulaires, une antérieure et les deux autres postéro-laterales'. Finally, Marcus (1977) has observed and drawn the innermost radular teeth with a small basal denticle in the curve between the cusp and basal plate. But this additional denticle has been noted by numerous earlier workers (Vayssière 1898, Thompson and Slinn 1959, Burn 1962, Thompson 1976). Vayssière (1898, p. 381) said: 'dents radulaires relativement peu nombreuses, unciformes, offrant chez les 15 à 20 premières un denticle sur le milieu de la face convexe de chacune'.

In conclusion it seems that the only character to unite the supposed species of *Gymnotoplax* is the perforate mantle and consequently the uncovered appearance of the shell. But *G. martensi* Pilsbry, upon further examination by Vayssière, was shown not to possess this character, and if this character is set aside, other species labelled as *Gymnotoplax* can be readily placed into already existing genera. It would appear that this character of a perforate mantle is an artifact caused by death of the individual and histolysis of the mantle above the shell before preservation. There is

no evidence to suggest it is a natural condition since the holotypes of both *G. americanus* and *G. barashi* were preserved when described. I doubt that any species of the Pleurobranchidae occurs in the living state with a perforate mantle; it follows therefore that it is not a natural condition for a pleurobranch to possess a shell which is partially or wholly uncovered.

ACKNOWLEDGEMENTS

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A NEW SPECIES OF *CUTHONA*
(GASTROPODA: OPISTHOBRANCHIA)
FROM THE BRITISH ISLES

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AND

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(Read before the Society, 20 May 1978)

Abstract: *Cuthona rubescens* n. sp. is described and illustrated. It is distinguished from *C. amoena* (Alder and Hancock, 1845) by consistent differences in pigmentation.

Recent collections of nudibranch molluscs from British waters included specimens of *Cuthona amoena* and animals similar in shape and ecology to *C. amoena*, but consistently differing in colour. Alder and Hancock (1855) stated that they had several specimens of '*Eolis amoena*' from Fowey Harbour in May 1847, most of which were 'typical' but 'one of the specimens had the bases of the papillae reddish and was blotched with opaque white down the front of each'. A later compilation by Walton (1908) described two captures from the North Sea that also differed from Alder and Hancock's (1845) type description of *C. amoena* in that 'the oral tentacles were white without the brown band', 'the red band on the rhinophores was broad' and 'the foot was more bilobed and produced into rounded lobes at the sides'.

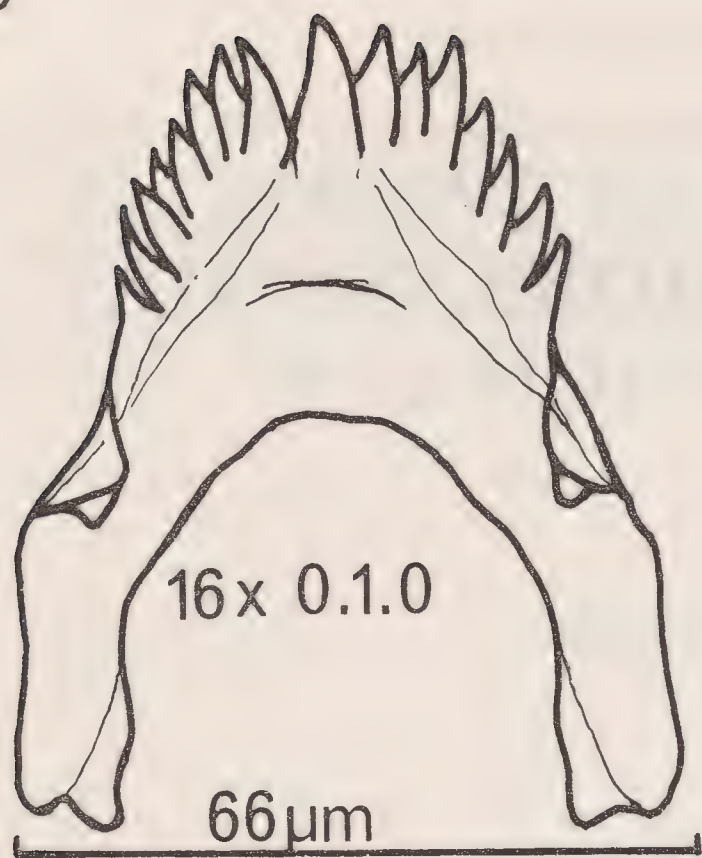
The genus *Cuthona* (recently enlarged by Miller (1977) so as to include *Trinchesia*) provides many examples of species that can most easily be separated on the basis of coloration. For example, *Cuthona caerulea* (Montagu 1804) and *C. viridis* (Forbes 1840) have similar radulae (in length and shape), similar reproductive systems (including the shape of the penial spine) and similar ceratal numbers and hepatic systems. Both Lemche (1964) and Miller (1958) initially thought that these two species were conspecific but later (Miller 1977, Lemche, personal communication) concluded that the colour differences warranted specific separation. The animals described here as a new species, *Cuthona rubescens*, have an equally close relationship to another species, *C. amoena*, but can be recognized immediately by reference to the external features noted by Alder and Hancock (1855) and Walton (1908). These authors had only three specimens altogether but our collections of over twenty individuals of both *C. amoena* and *C. rubescens* (with no intermediates) have convinced us of the validity of this new species although there is little anatomical evidence to separate them.

***Cuthona rubescens* sp. nov.** (Fig. 1a, b)

Material. June 1973, one specimen: 8 mm body length alive; North Haven (Skomer Island, Pembrokeshire).

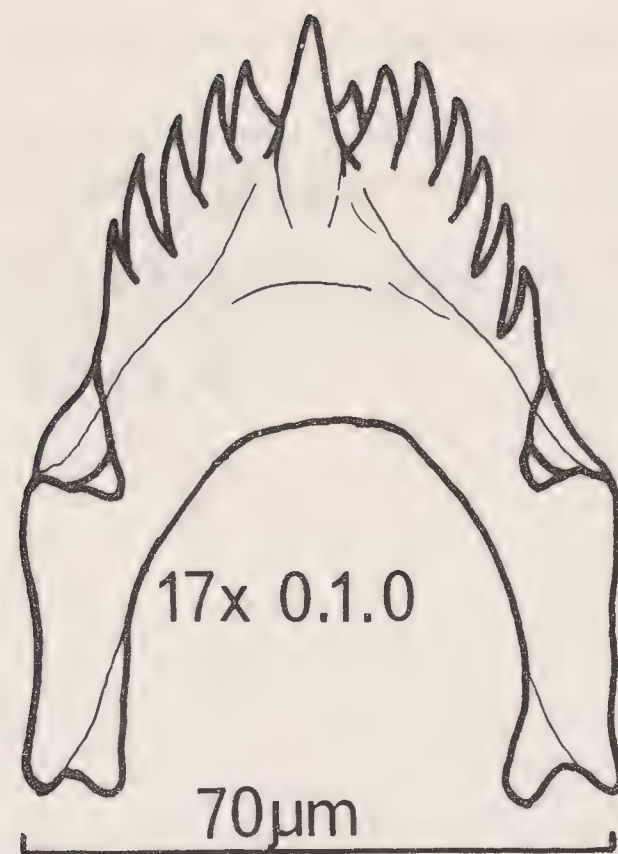
April and July 1975, six specimens: 4, 8, 8, 10, 10, 12 mm body lengths alive; Martinshaven, Garland Stone, Payne's Rock (Skomer Island, Pembrokeshire).

B



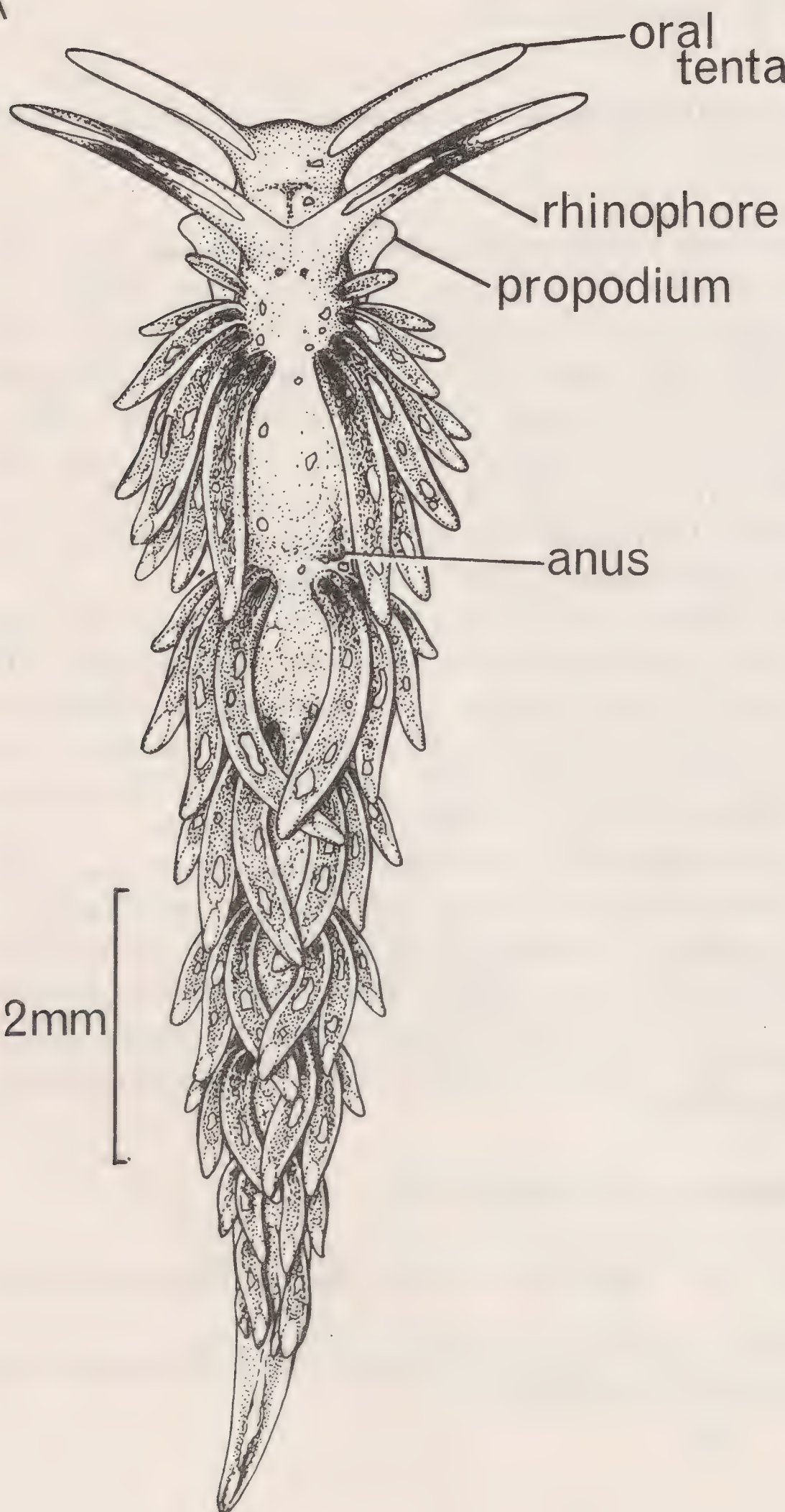
Cuthona rubescens

D

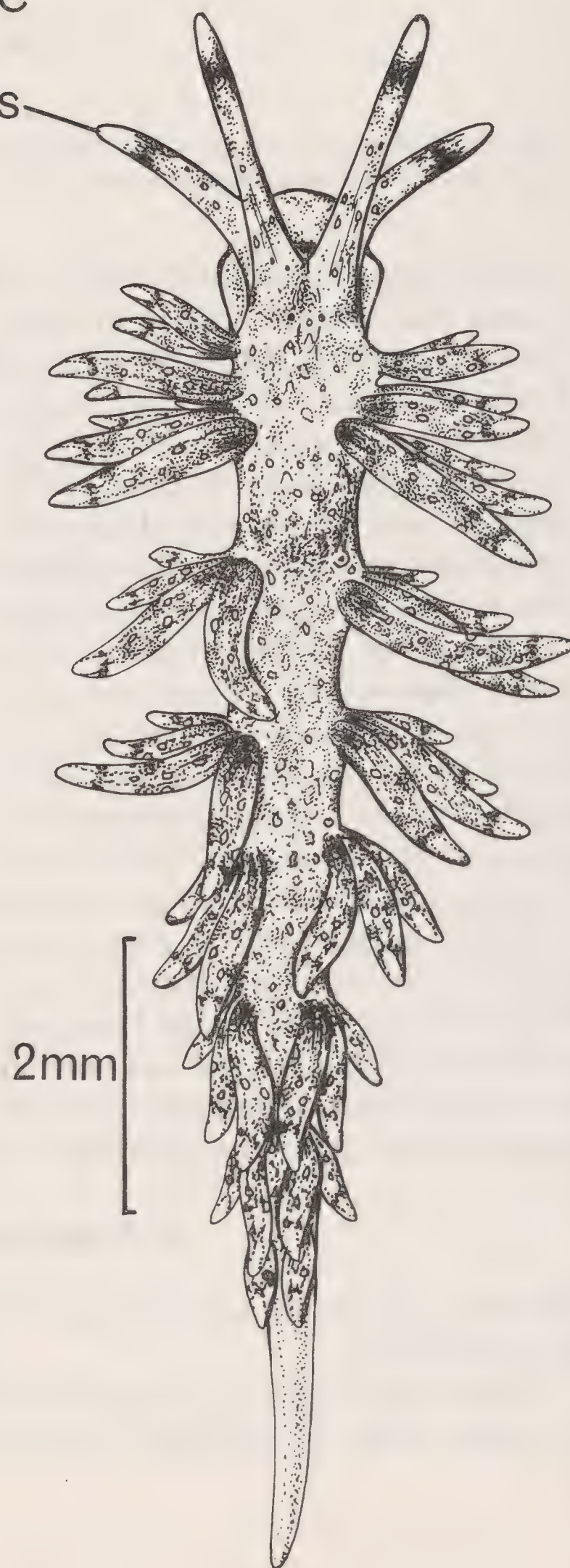


Cuthona amoena

A



C



May 1975, numerous specimens: 3 to 10 mm body lengths alive; Manacles Rock (Lizard Peninsula, Cornwall).

June 1975, six specimens: 4, 5, 5, 6, 6, 8 mm body lengths alive; Berry Head (Brixham) and Black Rock (Dartmouth, S. Devon).

August 1975, one specimen: colour photograph sent by the collector, C. Todd, Robin Hood's Bay, Yorkshire.

June 1977, one specimen: 6 mm body length alive; Gulland Rock (Padstow, N. Cornwall).

October 1977, one specimen: 4 mm body length alive; Scapa Flow (Orkney Island, Scotland).

May 1978, three specimens: 5, 12, 12 mm body lengths alive; St. John's Point (Donegal Bay, Eire). Holotype included.

All collections were made by scuba divers between 10 and 30 m below chart datum with the one exception found at extreme low water on the Yorkshire coast. Our animals were invariably on the calyptoblastic hydroid, *Halecium halecinum* although Walton (1908) obtained his specimens from *Sertularia argentea*. *C. amoena* also feeds on *Halecium halecinum*.

DESCRIPTION

External features. Mature specimens measure between 8 and 12 mm in length. Two blunt oral tentacles arise from the anterior corners of the head (Fig. 1a). The rhinophores are only slightly longer than the oral tentacles, smooth and tapering to a blunt tip. The eyes are clearly visible just behind the bases of the rhinophores and dark brown jaws can clearly be seen within the head. The cerata are cylindrical but narrow at their bases and rounded at their tips. They are set in up to eleven vertical rows with a maximum of six cerata in the two longest rows on either side of the pericardiac space. The cerata are arranged symmetrically on both sides of the body. The foot is narrower than the body but rounded and slightly produced at the anterior corners.

Opaque white ovotestis lobules are visible through the translucent skin and small patches of white pigment are often grouped anterior to the ceratal bases. The rhinophores are streaked by white pigment interrupted by a broad crimson band. The upper surface of each oral tentacle is covered by a continuous white streak and this character alone serves to distinguish even juvenile specimens from all other known British *Cuthona* species. The pigment on the cerata is better developed on the upper surfaces and consists of a crimson basal patch and white spots which occasionally form an incomplete ring at the level of the cnidosac. The digestive gland is usually dark olive green in freshly-collected specimens but becomes brown after a few days without food. The spawn consists of a white irregularly coiled thread wound around the stems of *Halecium halecinum*.

Anatomy. The uniseriate radula (Fig. 1b) of a 10 mm specimen consists of 16 teeth. Three other specimens, 12, 10 and 8 mm in length, have 17, 18 and 16 teeth, respectively. The radulae taper and the total number of denticulations varies between 17 at the growing end and 10 at the oldest end.

The penis is armed with a hook-shaped spine while the vas deferens has a short prostatic section. Serial sections of the reproductive system failed to provide evidence of any substantial differences from *C. amoena*.

Fig. 1. *Cuthona rubescens* sp. nov., a) dorsal view, b) largest radular tooth from a specimen measuring 10 mm body length alive.

Cuthona amoena, c) dorsal view, d) largest radular tooth from a specimen measuring 10 mm body length alive.

DIFFERENTIAL DIAGNOSIS

Only minor structural differences separate *Cuthona rubescens* sp. nov. from the closely related species, *C. amoena* (Fig. 1c). The pigmentation patterns are consistently distinct and can be summarized thus;

C. rubescens sp. nov.

- 1 White streak on oral tentacles.
- 2 Red band and pure white streak on rhinophores.
- 3 Little body pigment: a few scattered pure white spots.
- 4 Cerata with crimson bases and white surface patches

C. amoena (Alder and Hancock, 1845)

- Creamy-white pigment on oral tentacles interrupted by brown band.
Brown band and dull white pigment spots on rhinophores.
Dull brown pigment over most of the body interrupted by powdery white spots.
Cerata with brown bases and dull brown and white surface pigment.

The radulae of the two species are similar in length, shape and the number of denticulations (Fig. 1b, d). Ceratal numbers are usually greater in *C. rubescens* when animals of equivalent length are compared. The lateral propodial expansions are better developed in *C. rubescens* and the oral tentacles relatively longer.

DISTRIBUTION AND TYPE DESIGNATIONS

Our records extend from the very north of Britain (Scapa Flow) to the southernmost tip (Lizard Peninsula), with records from both the North Sea and the Atlantic coast. There are no records of animals that could be *C. rubescens* from anywhere outside British waters at present but the closely related *C. amoena* is recorded from the Mediterranean (Banyuls).

An intact specimen from St. John's Point, Donegal Bay, Eire, has been designated as the holotype and deposited at the British Museum (Natural History). A series of colour slides of the holotype has been deposited at the British Museum (Natural History) London; Royal Scottish Museum, Edinburgh; Ulster Museum, Belfast; Muséum National D'Histoire Naturelle, Paris, and the Universitetets Zoologiske Museum, Copenhagen.

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FERRISIA WAUTIERI (MIROLI)
(PULMONATA: ANCYLIDAE) NATURALIZED
IN SUSSEX, ENGLAND

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(Read before the Society, 20 May 1978)

Abstract: *Ferrissia wautieri* (Mirolli) has hitherto only been reported with certainty in England from greenhouses and aquaria. In 1977 it was discovered in a small stagnant pool away from houses in Sussex. Shells of *Ferrisia* can be distinguished by their small size and blunt apex which points to the left and has fine apical ridges.

In May and June, 1977 and March, 1978 small freshwater limpets were found in a small pool of stagnant water north-west of Longford Farm (51/428182) to the north of Barcombe Cross, East Sussex. They were originally identified as young of *Ancylus fluviatilis* Müller and the habitat was thought to be unusual. Brown (1977) reported the occurrence of *Ferrissia wautieri* (Mirolli 1960) possibly from a pond at Bishop's Waltham, Hampshire, and also in a water-lily tank at the Royal Botanic Gardens, Kew. Comparison of the Sussex specimens with *Ferrissia* collected in the highlands of Ethiopia by Dr. D. S. Brown in 1969 has confirmed they are of that genus, and they apparently do not differ from *F. wautieri*. This species has been reported from many European countries (Van der Velde and Roelofs 1977, Wautier 1974) and it may already have spread widely in southern Britain.

The Sussex locality is a small shallow pool not exceeding 10 m by 2 m in extent, situated in a small area of poor fen that is virtually surrounded by scrub through which a stream passes. The farm manager informed me that the pool was made about thirty years ago. In June 1977 the water was only about 10 cm deep but in March 1978 it was about 1 m in depth and much more extensive in area. It contains abundant vegetation of *Iris pseudacorus* and *Lemna minor*, with small quantities of *Alisma* sp. and filamentous alga. The only other mollusc found there is *Lymnaea glabra* (Müller), which is present (alone) in several other pools in the vicinity. Although the pool is man-made, it is situated in semi-natural vegetation more than a kilometre from the nearest house. *F. wautieri* is common in this pool on the submerged leaves and stems of *Iris*. Van der Velde and Roelofs (1977) report the species from eutrophic pools in Holland.

The largest shells from the Sussex site are over 4 mm long. The species is distinguished from small shells of *Acroloxus lacustris* (Linnaeus) by having the shell apex blunt and pointing to the left, whereas it is sharper and points to the right in *A. lacustris*. It is readily distinguished from *Ancylus fluviatilis* by the smaller, flatter shell with much finer apical ridges, which only become clearly visible at about $\times 40$ magnification. Van der Velde and Roelofs (1977, p. 74) give excellent photographs of the shell.

Specimens from the Sussex site have been presented to the British Museum (Natural History) and others are in private collections.

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A REVISION OF THE GENUS
REVOILIA BOURGUIGNAT 1881
(PROSOBRANCHIA: POMATIIDAE)

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Abstract: The group here dealt with includes several species previously attributed to *Otopoma* Gray 1850. The shells are small to medium sized prosobranchs inhabiting eastern Africa, southern Arabia, the island of Socotra and, by extension, a small area in western India. Their distribution and synonymy are reviewed and it is concluded that eleven species exist in two subgenera, *Revoilia* s.s. and *Socotora* Pallary 1925. Some previous authors have relied on the shape and size of the umbilicus as a specific indication, but our studies indicate that this, depending on the degree of callous closure, is merely a function of age and environment.

Under the generic name *Revoilia* Bourguignat 1881, we have placed a group of small to medium sized land prosobranchs referred by most previous authors dealing with them to *Otopoma* Gray 1850. When the latter author (1850, p. 35) published his genus *Otopoma* he designated no type species, but included under this name ten species of which the first was *Turbo foliaceus* Chemnitz, the second *Cyclostoma clausum* Sowerby and the third *C. listeri* Gray.

The first author positively to designate a type species for *Otopoma* was apparently Fischer (1885, p. 747), who selected *Cyclostoma listeri* Gray for this purpose. This species comes from Mauritius and is a form of *Tropidophora* (*Ligatella*). *Otopoma* Gray 1850 should therefore replace *Ligatella* von Martens 1880, as the oldest available name for this subgenus, which inhabits parts of south and east Africa and certain islands in the Indian Ocean, including Mauritius; it does not occur on Socotra nor in Arabia.

Gude (1921, p. 351) subsequently selected *Turbo foliaceus* Chemnitz as the type species of *Otopoma*, but overlooked the fact that on p. 91 of the same book he had already cited *T. foliaceus* as the type species of *Cyclohelix* Mörch 1852, a subgenus of *Cyclophorus* to which *T. foliaceus*, which comes from the Nicobar Islands and has a chitinous operculum, undoubtedly belongs.

Pallary (1925a, p. 230) correctly cited *C. listeri* Gray as the type species of *Otopoma*. Gray's generic name is therefore not applicable to the very different shells from Somalia, Socotra and Arabia, for which *Revoilia* Bourguignat 1881 (type species: *Cyclostoma naticoides* Récluz) is the oldest available name.

TAXONOMY

The genus *Revoilia* is a taenioglossid snail belonging to the Pomatiidae, a family which also includes *Pomatias*, *Tropidophora*, *Otopoma* and probably *Hartmannia*. Of these, *Pomatias* possesses a cartilaginous operculum composed of two plates and which is concamerated between them; *Tropidophora* is characterized by a carinated shell and *Hartmannia* has an elongated shell. The position of *Otopoma* has already been reviewed.

GEOLOGICAL HISTORY

The earliest appearance recorded of an undoubted species of *Revoilia* is from the Upper Eocene of the Department of Aude in southern France (Filhol 1877, p. 282), who records *Otopoma filholi* 'Bourguignat' from the Phosphorites du Quercy. No such species was described by Bourguignat, however, and it must therefore date from Filhol 1877 as *Revoilia (Socotora) filholi* (Filhol). The excellent illustrations which accompany Filhol's detailed description, together with the characteristic extension of the peristome across the umbilical cavity, leave us in no doubt that this Tertiary fossil is referable to *Revoilia (Socotora)*. The present location of the material is unknown to us.

The only other fossil records we have been able to trace are of an unidentified species of *Revoilia* from post-Pleistocene alluvium in Somalia and a very large example of the extinct *R. (S.) balfouri* (Godwin-Austen) obtained by Professor Balfour in a deposit of presumably similar age in Socotra. There does not seem to be any recorded occurrence of *Revoilia* in the Tertiary of North Africa, neither is the genus known from the Paris or Hampshire basins.

DISTRIBUTION

Revoilia is known to occur in northeast Kenya, the adjoining areas of Ethiopia, Somalia, the island of Socotra (but not on the nearby island of Abd el Kuri), and in the Arabian coastal belt in the Yemen. The occurrence of *R. clausa* (Sowerby) in northwest India is, in our opinion, probably due to human introduction.

Revoilia is essentially a genus of semi-arid areas and in Socotra it is found on the extensive limestone plains, especially to the east end of the island, where the limestone attains an elevation of over 700ft (215m). This island, with six species all endemic, would appear to be the main centre of development for the genus, the original connection having perhaps been with Somalia. The comparatively numerous and variable species found on the island are the usual result of long isolation and lack of competition, a characteristic of many island faunas. The species inhabiting East Africa and Arabia show a much closer relationship to each other than any of them do to the species found on Socotra.

Godwin-Austen (1881, p. 252) says of the land molluscan fauna of Socotra 'There is strong evidence that the island was once directly connected with Madagascar to the south. We know the great antiquity of that island, and it is not unreasonable to suppose that in Socotra, the Seychelles, Madagascar and Rodriguez we have the remains of a very ancient and more advanced coastline on the western side of the Indian Ocean, which line of elevation was probably continuous through Arabia towards the north. Such conditions would have admitted the extension of species across the area.'

Nevertheless, some connection also between Socotra and the African mainland in the past seems necessary to account for the occurrence of *Revoilia* in both areas, as well as *Otopoma* (= *Ligatella*) in Somalia, Socotra and Abd el Kuri. It is a curious fact that *Revoilia* should be unknown on the latter island.

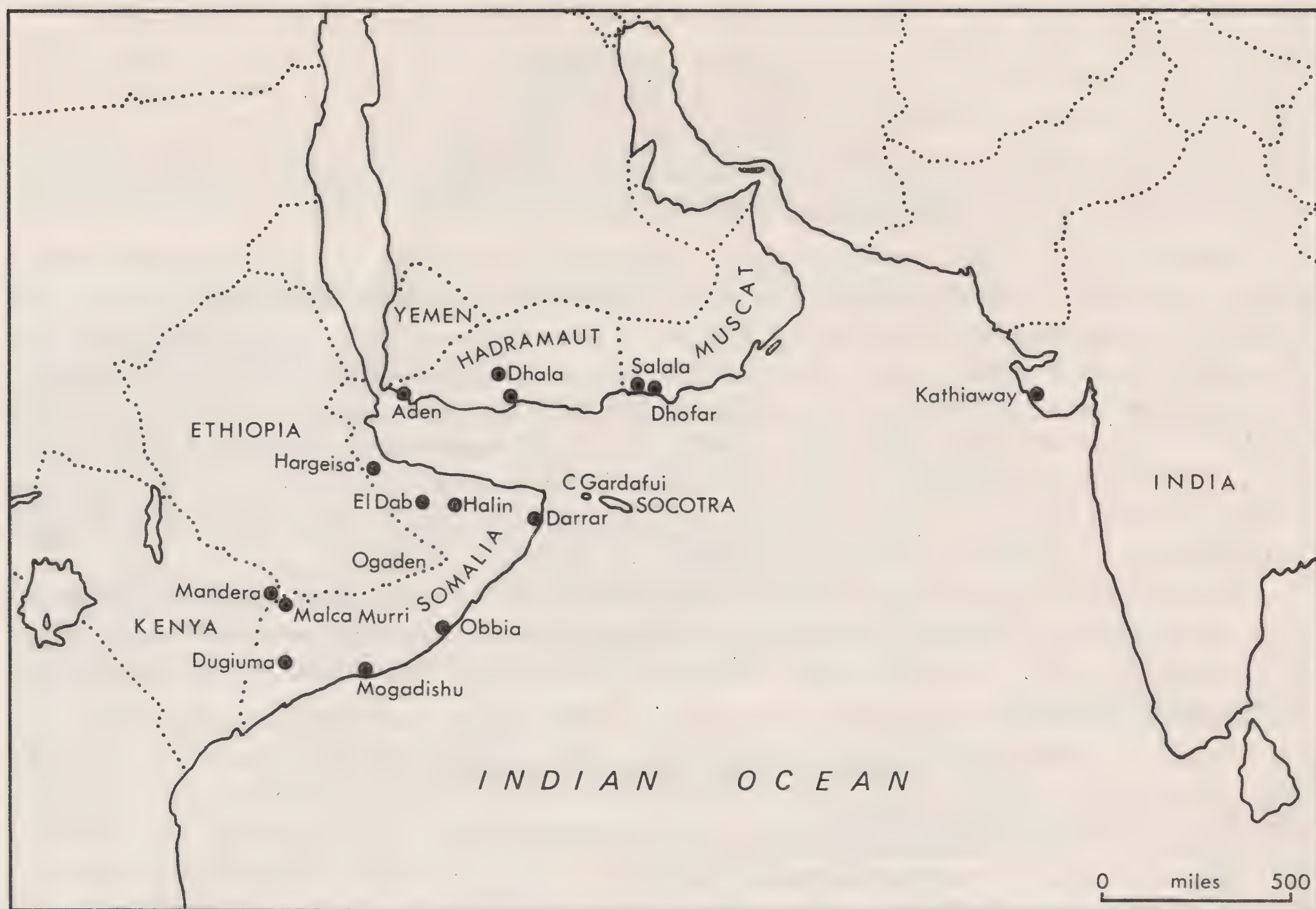


Fig. 1. Localities referred to in the text.

LOCALITIES

Somalia

- R. (S.) guillaini* (Petit)
 (= *naticopsis* Bgt., *perrieri* Bgt., *poirieri* Bgt.)
R. (S.) guillainopsis (Bgt.)
 (= *obbiensis* Connolly)
R. (Revoilia) milneedwardsi (Bgt.)

Arabia

- R. (S.) clausa* (Sowerby)
 (= *yemenica* Bgt., *hadramauticum* Melville and Ponsonby, *dhofarensis* M. and P., *consimile* M. and P., *pulchella* Pallary, *littlei* Pallary)
R. (S.) bentianum (Melville)
 (= *lucida* Pallary)

Socotra: six species
 Somalia: three species
 Arabia: two species

Socotra

- R. (S.) naticoides* (Récluz)
R. (S.) clathratulum (Récluz)
R. (S.) albicans (Sowerby)
 (= *complanatum* Godwin-Austen, *socotranum* Bgt.)
R. (S.) balfouri (Godwin-Austen)
R. (S.) auriculare (Griffith and Pidgeon)
R. (S.) conica (Godwin-Austen)

Ethiopia

- R. (S.) guillaini* (Petit)
R. (S.) guillainopsis (Bgt.)

Northeast Kenya

- R. (S.) guillaini* (Petit)

Northwest India

- R. (S.) clausa* (Sowerby)
 (= *hinduorum* Blanford)

Ethiopia: two species
 NE Kenya: one species
 NW India: one species

Abd el Kuri: none

SYSTEMATIC DESCRIPTIONS

Family Pomatiidae

subfamily Pomatiinae

Genus *Revoilia* Bourguignat 1881

(Type species by monotypy, *Revoilia milneedwardsi* Bourguignat 1881). = *Otopoma* auctt., non Gray 1880, *Georgia* Bourguignat 1882 non Baird and Gerard 1853.

Pallary (1925a p. 230) correctly listed *C. listeri* Gray as the type species of *Otopoma*: Gray's generic name is therefore not applicable to the very different shells from Somalia, Socotra and southern Arabia for which *Revoilia* Bourguignat is the oldest available name. These shells are discoidal, the apex slightly raised, the whorls sculptured with numerous distinct spiral threads; Bourguignat characterized the genus as having 'the umbilicus wide open in juveniles, but in the adult always entirely filled with a thin covering of callus spreading from the columellar border'. However, we have seen specimens of *R. auriculare* (Griffith and Pidgeon) in particular, in which every variation from an open umbilicus to a completely closed one was present. Similar variations are to be found among specimens of *R. naticoides* (Récluz).

The aperture is circular, peristome continuous and having a marginal dilatation spreading over the periphery of the last whorl and on to its upper region. The upper and lower callosities of the peristome in the columellar area thus give a distinctive saddle-like appearance on the underside of the shell.

Revoilia (Revoilia) milneedwardsi Bourguignat 1881.

1881 *Revoilia milne-edwardsi* Bourguignat: 9

1882 *Revoilia milne-edwardsi* Bourguignat; Bourguignat: 88, pl. 3, figs. 57-59

1951 *Otopoma (Revoilia) milne-edwardsi* Bourguignat; Bacci:23.

The species is endemic to Somalia in the Cape Gardafui area where shells were collected by Revoil between Tohen and Binnah and sent to Bourguignat. The type is possibly in the Paris Museum. Through the kindness of Mr. D. Heppell we have been able to examine one specimen of this apparently rare species. The shell, though worn, is almost identical to Bourguignat's beautifully figured type in respect both of appearance and size. Its height is 15.5mm and maximum diameter 22.5mm. It is noticeably flattened, with a short spire and large last whorl; the very wide umbilicus is completely filled with a pad of callus. The strong spiral sculpture which covers the entire shell together with the flared and crenulate outer lip separate this species from all other known species of *Revoilia* and we consider the retention of Bourguignat's subgenus *Revoilia* justifiable on these grounds.

Subgenus *Socotora* Pallary 1925

(Type species, by original designation, *Cyclostoma albicans* Gray and Sowerby, 1839) = *Arabia* Pallary, 1925 (type here selected *Otopoma bentianum* Melville, 1895).

Georgia Bourguignat, 1882 is preoccupied by *Georgia* Baird and Gerard, 1853, a snake, and is thus not available. The next subgeneric name in line is *Socotora* Pallary. Pallary (1925, p. 231) created two groups, *Socotora* and *Arabia*, which he apparently intended to have the status of subgenera, for species of *Revoilia* in which the umbilicus was very wide and deep (*Socotora*) and those in which it is completely closed (*Arabia*). However, as already mentioned, every variation occurs from a closed to an open umbilicus in a number of species of *Revoilia* and we can see no justification for retaining the distinction.

Definition: Ventricose-conoid shells with swollen, rounded whorls, spire turbinate, the umbilicus sometimes completely covered by an outgrowth of the columellar lip, but widely open in some species. Aperture nearly circular, peristome not continuous, being offset at the point of insertion of the inner lip. Operculum calcareous, moderately thick, convex on the outside, with a depressed nucleus; having four whorls, the last rapidly increasing in size, the sutures thickened; interior concave, covered with a thin, transparent membrane.

The animal: Godwin-Austen (1897) examined the animal of *G. naticoides* and *G. clathratulum* and reported that they were similar in anatomical details. On p. 29 he says: "Animal having a short, divided foot; margin of the mantle free in front; the muzzle divided into two lobes. Eyes prominent on the outer side of the tentaculae near the base. The male organ is situated close to and just above, the rectum at the right posterior side of the branchial chamber. The teeth of the radula are narrow and elongate with minute serrations, arranged 3-1-3. No buccal plates."

Revoilia (Socotora) clathratula (Récluz 1843) Plate 1, figs. 1-2.

- 1843 *Cyclostoma clathratula* Récluz: 3, p. 74.
- 1846 *Cyclostoma clathratula* Récluz, Pfeiffer: 38, pl. 5, figs. 5-6.
- 1847 *Cyclostoma clathratula* Récluz, Sowerby: 17, pl. 23, figs. 15-16.
- 1852 *Cyclostoma clathratula* Récluz, Pfeiffer: 164.
- 1862 *Cyclostoma clathratula* Récluz, Reeve: pl. 18, figs. 116a-b.
- 1881 *Otopoma clathratulum* var. *minor* Godwin-Austen: 255.
- 1882 *Otopoma clathratulum* var. *minor* Godwin-Austen, Bourguignat: 62.
- 1883 *Otopoma clathratulum* var. *minor* Godwin-Austen, von Martens: 142.
- 1884 *Otopoma clathratulum* var. *minor* Godwin-Austen, Crosse: 363.
- 1897 *Otopoma clathratulum* var. *minor* Godwin-Austen, Godwin-Austen: 30, pl. 7, fig. 6 (Anatomy).
- 1903 *Otopoma clathratulum* var. *minor* (Récluz) [sic], E. A. Smith: 142.

The original description appears, after quoting a number of generic characteristics, to be based on the colour pattern of the shell, which possesses brownish transverse bands. The uppermost whorls have a black zone at the base and the last whorl is bordered with pale orange fringed with brown; the aperture is orange within. These characteristics appear to be constant enough to identify the species.

The shell is endemic to Socotra, where it appears to be very common in places. The type material is probably in the Paris Museum, that of var. *minor* is in the British Museum (Natural History), London.

According to Smith (1903, p. 142), shells of this species range from 15 to 25 mm in diameter; we have seen no specimen greater than 18.5 mm, but the variation in size is of no importance from a varietal point of view. All sizes of the typical form were collected by Forbes and Grant, the smallest examples, judging from their thickened peristome, being as fully adult as the largest. The var. *minor* Godwin-Austen (1881, p. 225) differs only in the absence of spiral colour lines, the shape and sculpture being identical. The size quoted by the author, 18 mm in major diameter, is altogether misleading as the largest specimens placed by him in this variety measure 25 mm, the largest size for the nominate form. All examples have the dark purplish zone above the suture upon the upper part of the spire.

Regarding the animal, Godwin-Austen (1897, p. 30) says: 'the male organ is in the same position [as in *R.(S.) naticoides*] but has a more elongate form and is of the same diameter throughout. The radula is precisely like that of *naticoides*'

The large series of specimens we have examined show considerable variation in spire height and in depth of colour, as well as in the extent to which the expansion of the parietal callus covers the umbilicus.

Revoilia (Socotra) guillaini (Petit 1850) Plate 1, fig. 3.

- 1850 *Cyclostoma guillaini* Petit: 51, pl. 4, fig. 3.
- 1881 *Otopoma perrieri* Bourguignat: 4.
- 1881 *Otopoma poirieri* Bourguignat: 6.
- 1882 *Georgia guillaini* (Petit), Bourguignat: 69, 72, pl. 3, fig. 49.
- 1882 *Georgia naticoides* Bourguignat: 71, pl. 3, figs. 43-48.
- 1882 *Georgia perrieri* (Bourguignat), Bourguignat: 73, pl. 3, figs. 50-51.
- 1882 *Georgia poirieri* (Bourguignat), Bourguignat: 74, pl. 3, figs. 54, 56.

- 1882 *Georgia revoili* Bourguignat: 76, pl. 3, figs. 52, 53.
 1889 *Georgia naticopsis* Bourguignat: 143.
 1889 *Georgia perrieri* (Bourguignat), Bourguignat: 144.
 1889 *Georgia revoili* Bourguignat, Bourguignat: 144.
 1889 *Georgia guillaini* (Petit), Bourguignat: 144.
 1909 *Georgia poirieri* var. Kobelt: 40, pl. 9, figs. 1-3.
 1928 *Otopoma* (*Georgia*) *naticopsis* (Bourguignat), Connolly: 16.
 1928 *Otopoma* (*Georgia*) *revoili* (Bourguignat), Connolly: 16.
 1928 *Otopoma* (*Georgia*) *guillaini* (Petit), Connolly: 18.
 1928 *Otopoma* (*Georgia*) *perrieri* Bourguignat, Connolly: 19.
 1951 *Otopoma* (*Georgia*) *guillaini* (Petit), Bacci: 22.
 1951 *Otopoma* (*Georgia*) *naticopsis* (Bourguignat), Bacci: 22.
 1951 *Otopoma* (*Georgia*) *perrieri* Bourguignat, Bacci: 22.
 1951 *Otopoma* (*Georgia*) *revoili* (Bourguignat), Bacci: 22.
 1954 *Otopoma* (*Georgia*) *perrieri* Bourguignat, Pain: 400.
 1954 *Otopoma* (*Georgia*) *guillaini* (Petit), Pain: 400.
 1960 *Otopoma* (*Georgia*) *perrieri* Bourguignat, Verdcourt: 224.
 1960 *Otopoma* (*Georgia*) *naticopsis* (Bourguignat), Verdcourt: 225.
 1963 *Otopoma* (*Georgia*) *perrieri* Bourguignat, Verdcourt: 403.
 1963 *Otopoma* (*Georgia*) *naticoides* (Bourguignat), Verdcourt: 404.

This is a bluish-white shell with circular thickened aperture, barely angulate above and yellow internally. The shell is strongly calloused below, sometimes sufficiently to fill the large umbilicus. The species described by Bourguignat seem to differ only in minor and inconstant variations in proportion and sculpture.

The species is found in Somalia, Ethiopia and the extreme northeast of Kenya. A type locality was never designated and Mogadishu, Somalia is here selected. The adult shells examined vary in height from 22 to 31.5 mm and in diameter from 23 to 32.5 mm.

Examination of a considerable amount of material from Somalia, some of it variously referred to *perrieri* or *naticoides* depending apparently on the size of the specimen, has convinced us that all represent but one variable species, for which the oldest name is *guillaini* Petit. The type of this shell is in the collection of the Journal de Conchyliologie in Paris, and is noticeably larger than the figure, which is a poor one. Bourguignat (1882, pl. 3, fig. 49) gives an excellent engraving of this species, together with representations of his own supposed new species *naticopsis*, *perrieri*, and *poirieri*; of these, the last two are certainly synonymous, as recognized by Connolly (1928, p. 19) after specimens from Somalia had been compared with the original material in the Paris Museum. Bourguignat separated his two species from *guillaini* as having reflexed instead of a merely thickened peristome; he also stated that the suture of *perrieri* was merely impressed, in contrast to that of *poirieri* which was canaliculate. Like Connolly, we have seen no specimen with a canaliculate suture, this being invariably impressed and sometimes strongly margined.

Most of the examples examined are more or less bleached, but a large series collected by W. Feather in 1909 and now in the Royal Scottish Museum, Edinburgh, are beautifully fresh. These were obtained near Mandara in what was then British Somaliland; they show much weaker sculpture than the ones which have lost their periostracum. They are a pale tawny brown above, with a dark brown band commencing at the apex and continuing between the suture and the periphery; below this is a second band a short distance from the other. This series of shells is generally smaller than the ones collected by Hemming (which average 17×20 mm) and is in fact remarkably constant in this respect.

In fresh examples from Mogadishu there are eight narrow dark bands on the upper surface of the last whorl between the suture and the broad band, and beneath this the shell is white. In these examples, which closely resemble Bourguignat's figure of *guillaini*, the extension of the peristome covering the umbilicus is very thin indeed and frequently broken away. The spiral sculpture, weakly developed in the Mandara examples, shows strongly above the periphery of

the last whorl in those from Mogadishu, although they are smooth beneath. In all specimens examined the first one and a half whorls are smooth, bluish in colour and with the dark brown band plainly visible even at the apex.

Although typical examples of *R. (S.) naticopsis* are considerably larger and have a strong and often malleated sculpture above the periphery of the last whorl, intermediate examples connecting these with *guillaini* and *perrieri* are not uncommon and occur in more than one locality; *naticopsis* would appear to have been founded merely on large examples of *guillaini* and in view of the variability exhibited by this highly polymorphic species, we can see no justification for retaining *naticopsis* even as a subspecies.

Verdcourt (1963, p. 404) points out that specimens he identified as *Otopoma naticopsis* are obviously all conspecific and that apical whorls are uniform throughout; the shells vary in size, however, from 19.5 × 19.0 mm to 26.0 × 18.5 mm, and the smallest is indistinguishable from *O. perrieri* (Bourguignat). A series of shells identified as *perrieri* in the Kenya Museum, Nairobi, from Ogaden, Ethiopia, have the umbilicus quite open although they are adult. They seem indistinguishable from specimens collected at El Dab, Somalia, identified by Verdcourt (1960, p. 226) as *Ligatella cecionii* Bacci, which itself may prove to be a variant of *R. (S.) guillaini* since in some areas several umbilicate examples may be found together. Since we have not seen the material, nor any examples of *L. cecionii*, we are at present unable to venture an opinion in the matter.

Although Connolly (1928, p. 16) maintained *O. revoili* (Bourguignat), he noted that it should be considered at most only as a variety of *perrieri*. This shell is typically smaller and flatter by comparison with *perrieri*, but seems to merge gradually into it. A series of typical examples from Dugiuma, Somalia show the closed umbilicus, but with a distinct cavity as mentioned by Bourguignat in his original description. Shells of this type, however, with a proportionately larger body whorl are also found among normal examples of *perrieri*, presenting yet another example of the variation to be found within the range of *R. (S.) guillaini*. It is worth bearing in mind that in many variable European species, such as *Ceruella virgata*, size differences are not considered of much importance.

For additional localities in Somalia, Ethiopia and northeast Kenya see Verdcourt (1960, 1963), based on extensive material in the Kenya Museum, Nairobi and the Musée Royal de l'Afrique Centrale, Tervuren.

The radula (of *naticopsis*) is said by Connolly (1928, p. 17) to be about 9.6 mm in length and to consist of 350 transverse rows of teeth.

Revoilia (Socotora) guillainopsis (Bourguignat 1882) Plate 1, figs. 4–5.

- 1853 *Cyclostoma guillaini* Pfeiffer: pl. 34, figs. 7–8 (*non* Petit 1850)
- 1862 *Cyclostoma guillaini* Reeve: pl. 19, fig. 126 (*non* Petit 1850)
- 1882 *Rochebrunia guillainopsis* Bourguignat: 81.
- 1889 *Rochebrunia guillainopsis* Bourguignat, Bourguignat: 146.
- 1928 *Otopoma (Georgia) guillainopsis* (Bourguignat), Connolly: 17.
- 1928 *Otopoma (Georgia) guillainopsis obbiensis* Connolly: 18, pl. 3, fig. 6.
- 1951 *Otopoma (Georgia) guillainopsis* (Bourguignat), Bacci: 22.
- 1951 *Otopoma (Georgia) guillainopsis obbiensis* Connolly, Bacci: 22.
- 1954 *Otopoma (Georgia) guillainopsis* (Bourguignat), Pain: 400.
- 1960 *Otopoma (Georgia) guillainopsis* (Bourguignat), Verdcourt: 224.

The original description laid stress on the open umbilicus which is, as we have already submitted, purely adventitious; the rest of the features described are comparative, e.g. it has a chalkier, thicker shell than *guillaini*, is more ventricose, has more elevated spire and more rounded aperture. Connolly created his subspecies *obbiensis* on a local race from Obbia near

Mogadoxa, Somalia, having a closed umbilicus, coarse spiral sculpture and sometimes a yellow band.

This species comes from Somalia and Ethiopia, and examples from several localities in both countries have been seen by the authors. A review of these appears to indicate that the species can be maintained.

The range of dimensions for adult shells is: in height 23–29 mm. in diameter 13–16.5 mm, with $5\frac{1}{2}$ whorls. Bourguignat (1882, p. 81) commences his description of the species with the statement that ‘. . . it is perhaps not related to the true *guillaini* of Petit’, but Connolly (1928, p. 17) states that the Mogadishu shells include specimens with the umbilicus entirely closed while in others it is more or less open. He described *obbiensis* from the former batch.

In all the adult specimens we have seen, the umbilicus is entirely closed by the extension of the peristome across it. We can only conclude, therefore, that perforate or partially perforate shells are immature, closure representing the adult state.

The shell of typical adult *guillainopsis* is conical, thick, imperforate, solid, somewhat glossy, the upper whorls smooth, striated below and in large specimens from Garbuen, malleated on the body whorl. The suture is impressed, aperture rounded, outer lip thickened, up to 3 mm across the rim in some large shells. All examples seen were white, some with traces of red or orange colour on the spire. Connolly mentions a specimen girdled by a yellow subperipheral band and a few examples are bluish tinged, the interior of the aperture being orange-yellow. In this species the shell is noticeably higher than wide and differs from *guillaini* in this respect as well as in being far thicker.

It should be noted that in Pfeiffer's figures (1853, pl. 34, figs. 7–8), which Bourguignat designated as the type of *guillainopsis*, the shell is white, conical, with the umbilicus only partly covered; this shell is therefore probably immature.

Revoilia (Socotora) naticoides (Récluz 1843) Plate 1, fig. 6.

- 1843 *Cyclostoma naticoides* Récluz: 3, pl. 73.
- 1846 *Cyclostoma naticoides* Récluz, Pfeiffer: 37, pl. 5, figs. 1–4.
- 1847 *Cyclostoma naticoides* Récluz, Sowerby: 117, pl. 26 figs. 108–9.
- 1859 *Tropidophora (Otopoma) naticoides* (Récluz), Chenu: 492, fig. 3640.
- 1862 *Cyclostoma naticoides* Récluz, Reeve: pl. 18, fig. 117a–b.
- 1881 *Otopoma naticoides* (Récluz), Godwin-Austen: 252, pl. 27, figs. 1, 1a.
- 1882 *Georgia naticoides* (Récluz), Bourguignat: 67.
- 1882 *Georgia austeni* Bourguignat: 68.
- 1884 *Otopoma naticoides* (Récluz), Crosse: 361.
- 1898 *Otopoma naticoides* (Récluz), Godwin-Austen: 29, pl. 67, figs. 1–5.
- 1903 *Otopoma naticoides* (Récluz), E. A. Smith: 138, figs. a–c.
- 1926 *Otopoma naticoides* (Récluz), Pallary: 104–106, pl. 7, figs. 1–4.
- 1969 *Otopoma naticoides* (Récluz), Salvat: 744.

The shell is very solid and very globose; the extreme apex is commonly decollate. The operculum is situated well within the aperture and is slightly concave in front, shelly and with a subcentral nucleus. It is a large and distinctive species, a typical adult measuring about 45–50 mm in height and much the same in diameter; its strongly marked transverse irregular growth lines and noticeably turbinate form make it unlikely to be confused with any other species.

The interior of the aperture in fresh examples is of a deep orange colour, the remainder of the shell white, with a distinctive gloss. There is some variation in the development of the wing-like inner expansion of the peristome; in some examples this is sufficient completely to fill in the umbilicus and in others coverage is only partial. This was so in the case of the somewhat thin specimen figured by Godwin-Austen and described by Bourguignat as *G. austeni*, but there is a complete gradation between this form and the more typical *naticoides* in which the umbilicus is completely filled by a pad of callus.

Godwin-Austen (1897, p. 29) gives a good description of the anatomy of this species.

R.(S.) naticoides is endemic to the island of Socotra where it is very common on the limestone plain in several localities.

Revoilia (Socotora) albicans (Gray and Sowerby 1839) Plate 1, figs. 7–8.

- 1839 *Cyclostoma albicans* Gray and Sowerby: 146, pl. 38, fig. 30.
- 1846 *Cyclostoma albicans* Gray and Sowerby, Pfeiffer: 87, pl. 11, figs. 13–14.
- 1847 *Cyclostoma albicans* Gray and Sowerby, Sowerby: 118, pl. 36, figs. 110–112.
- 1862 *Cyclostoma albicans* Gray and Sowerby, Reeve: pl. 18, fig. 20.
- 1881 *Otopoma complanatum* Godwin-Austen: 254, pl. 27, figs. 3, 3a.
- 1881 *Otopoma clathratulum* var. *socotrana* Godwin-Austen: 254, pl. 27, fig. 4.
- 1882 *Otopoma complanatum* Godwin-Austen, Bourguignat: 61.
- 1882 *Otopoma socotranum* Bourguignat: 64.
- 1903 *Otopoma complanatum* Godwin-Austen, E. A. Smith: 140, pl. 12, figs. 4–5.
- 1903 *Otopoma socotranum* Bourguignat, E. A. Smith: 141, pl. 12, fig. 6, text-figs. a–b.

A medium-sized shell, as the species of *Socotora* go, adults varying from about 27–35 mm high and about 4 mm more in diameter. It is always white, but occasional specimens are tinged with purple; minutely and regularly sculptured with fine spiral ribbing, sometimes with signs of transverse grooves also, and usually malleated below. The operculum is situated very close to the peristome.

Godwin-Austen considered his var. *socotrana* to be closely allied to *O. clathratulum* Récluz, as figured by Reeve in the *Conchologica Iconica* pl. 18 fig. 116b. The basis for the variety was two rather faded examples, but fresh shells later obtained from the same locality by Mrs. Bent exhibit a style of coloration almost identical to that of the lineated form of *complanatum*. One of these fresh examples is beautifully figured by Smith (1903) and confirms that the variety is perfectly distinct from *clathratulum* s.s.

Bourguignat raised this variety to specific rank as *O. socotranum*, his action being founded only upon Godwin-Austen's description and figures, no specimen having been examined by him. Although undoubtedly resembling *clathratulum*, the shells called *socotranum* may be distinguished by a more contracted umbilicus resulting from the body-whorl being more tightly coiled and the spire more elevated. None of the specimens of *socotranum* we have examined possess the short dentiform prominence on the columellar margin which sometimes occurs in that variety according to Godwin-Austen (1881). It would appear from the above that var. *socotranum* is attributable to *albicans* rather than *clathratulum*. *R.(S.) albicans* is endemic to Socotra, and according to Balfour (Godwin-Austen 1881, p. 254) it is 'very common on limestone plains from more than one locality, and common towards the east end of the island; all the land in this region is elevated over 700 ft and is of limestone.'

Revoilia (Socotora) balfouri (Godwin-Austen 1881), Plate 2, fig. 1.

- 1881 *Otopoma balfouri* Godwin-Austen: 253, pl. 7, fig. 2.
- 1882 *Otopoma balfouri* Godwin-Austen, Bourguignat: 60.
- 1884 *Otopoma balfouri* Godwin-Austen, Crosse: 362.
- 1903 *Otopoma balfouri* Godwin-Austen, E. A. Smith: 139, figs. a–b.
- 1925a *Socotora balfouri* (Godwin-Austen), Pallary: 231.

This is another species endemic to Socotra, reported to have been common on land towards the east end of the island; these parts are elevated to over 700 ft (215 m) and are made of limestone.

The holotype is in the British Museum, Natural History, London, with paratypes in the National Museum of Wales, Cardiff and the Pain collection, ex Connolly.

Godwin-Austen (1881, p. 253) noted the resemblance between *R. (S.) auriculare* (Gray), of unknown habitat, and *R. (S.) balfouri*; the latter is larger (about 55 mm in diameter and 22 mm high), more coarsely sculptured, with a very wide and deep umbilicus and lacking the extension of the peristome across the umbilicus, this being replaced by a small notch. From *R. (S.) albicans* it differs in being strongly ribbed, with the apex decollate in all specimens seen. Godwin-Austen recorded a dwarf variety with a maximum diameter of 35 mm, but we have seen no specimens of it.

The large size, strong, regular ribbing, decollate apex and very wide and deep umbilicus serve to separate *R. (S.) balfouri* from all other Socotran species of *Revoilia*. Although said to be common by Professor Balfour, this species was not met with by the Forbes Expedition, nor does it seem to have been subsequently collected. Only dead shells appear to have been obtained by the discoverer, so that the animal and operculum are unknown. All examples we have examined have the appearance of being dead and weathered.

Revoilia (Socotora) auriculare (Griffith and Pidgeon 1834) Plate 2, fig. 4–5.

1834 *Cyclostoma auriculare* Griffith and Pidgeon: pl. 28, fig. 5.

1847 *Cyclostoma candidum* Sowerby: 117, pl. 26, figs. 110–112.

1852 *Cyclostoma candidum* Sowerby, Pfeiffer: 172, pl. 25, fig. 6.

1862 *Cyclostoma auriculare* Griffith and Pidgeon, Reeve: pl. 18, figs. 118a–b.

No definite locality is known for this species, but it is undoubtedly a *Revoilia (Socotora)* allied to *R. (S.) naticoides* and most probably comes from Socotra. It is curious however, that none of the expeditions to that island obtained the species because nothing like it is known to occur in Somalia or Arabia.

Sowerby mentioned a variety in which the umbilical callus is much smaller and reflected; this may possibly refer to the species subsequently described by Godwin-Austen as *Otopoma balfouri*. The resemblance was noted by Smith (1881), but he was in error in stating that the sculpture is coarser and more distinct in *auriculare*, since the reverse is the case.

R. auriculare is readily recognizable from the original picture of Griffith and Pidgeon and it was subsequently beautifully figured by Reeve (1862) from a specimen in the Cuming collection, which may still be preserved in the British Museum, Natural History. The sculpture is finer than in *R. balfouri* and lacks the strong growth lines and malleated surface of *R. (S.) naticoides*. The expansion of the peristome partly conceals the umbilicus, which is wide and deep and in this respect *auriculare* forms a link between the other two species, for in *balfouri* the expansion is reduced to a very slight protuberance and in *naticoides* it often completely covers the umbilicus.

In spite of its intermediate position, *R. (S.) auriculare* is nevertheless distinct, and we are obliged to retain it as a valid species. Shells seen measure about 38 mm high and 40 mm in diameter.

Revoilia (Socotora) conica (Godwin-Austen 1881) Plate 2, fig. 7.

1881 *Otopoma conicum* Godwin-Austen: 255, pl. 28, figs. 1–1b.

1882 *Rochebrunia conica* (Godwin-Austen), Bourguignat: 84.

1884 *Otopoma conicum* Godwin-Austen, Crosse: 364.

1903 *Otopoma conicum* Godwin-Austen, E. A. Smith: 142 (fig. on p. 143).

This is another 'lost' species from Socotra, obtained there only by Professor Balfour from the Plain in the vicinity of Gollonsir Village. It is one of the smallest species in the genus, the height of adult shells averaging 13 mm and the diameter slightly more. It is distinctly umbilicate, conoidal and moderately thick; the first two whorls are smooth, the remainder sculptured with spiral ridges which are crossed by delicate longitudinal threads. The aperture is circular, angled

above, the peristome thin and continuous, but not reflected. All the specimens we have seen are off-white in colour. Smith (1903, p. 143) said of the type material 'These appear to be bleached shells, for a careful examination of them reveals faded colour markings upon the upper surface.' The distinctive surface sculpture and conical shape serve to separate this species from other Socotran *Revoilia*. It is apparently rare, and was not obtained by the Forbes Expedition. The animal is unknown.

Revoilia (Socotora) clausa (Sowerby 1847) Plate 2, fig. 6.

- 1847 *Cyclostoma clausum* (Sowerby: 128, pl. 31, figs. 266–267.
- 1850 *Cyclostoma clausum* Sowerby, Pfeiffer: 147, pl. 20, figs. 13, 15.
- 1852 *Cyclostoma clausum* Sowerby, var. 'B' Pfeiffer: 180.
- 1853 *Cyclostoma clausum* Sowerby, var. 'B' Pfeiffer: 330, pl. 42, figs. 13–15.
- 1859 *Otopoma clausum* (Sowerby), Benson: 92, 95.
- 1864 *Otopoma hinduorum* Blanford: 464.
- 1870 *Cyclostoma (Otopoma) hinduorum* (Blanford), Blanford: 12, pl. 3, fig. 6.
- 1882 *Georgia clausa* (Sowerby), Bourguignat: 70.
- 1882 *Georgia yemenica* Bourguignat: 70.
- 1889 *Georgia yemenica* Bourguignat, Jousseume: 206.
- 1896 *Otopoma hadramauticum* Melville and Ponsonby 2, pl. 1, figs. 1–3.
- 1896 *Otopoma consimile* Melville and Ponsonby: 2, pl. 1, figs. 5–7.
- 1896 *Otopoma dhofarensis* Melville and Ponsonby: 2, pl. 1, figs. 9–11.
- 1921 *Otopoma hinduorum* Blanford, Gude: 351 (fig. in text).
- 1925a *Otopoma littlei* Pallary: 226, pl. 35, figs. 1–3.
- 1925a *Otopoma hadramauticum* Melville and Ponsonby, Pallary: 226, pl. 35, fig. 7.
- 1925a *Georgia pulchella* Pallary: 232, pl. 35, fig. 15.
- 1941 *Arabia hadramautica* (Melville and Ponsonby), Connolly: 34.

The species occurs in south Arabia—Hadramaut and the Yemen; also in Kathiawar, northwest India. For additional records in south Arabia see Pallary 1925a and Verdcourt 1960. A type locality was not designated and Dhofar, 800 miles east of Aden, is selected here. Of the type material, the location of *clausa* is unknown; *hinduorum* is in the British Museum, Natural History, as are those of *dhofarensis*, *consimile* and *hadramauticum* with paratypes of the latter in the National Museum of Wales; *yemenica* is in the Paris Museum; *littlei* and *pulchella* in the Brussels Museum.

The original descriptions of the various so-called species quote shells which are variously depressedly orbicular, globose-turbinate, depressed-conical, conical with rounded whorls, globose-conical, etc. These and similar terms, although hallowed by the conventions of species description, are in themselves quite useless when trying to distinguish between closely similar shells. Stress is laid in each case on the presence or absence of parietal callus, and altogether there is in no case any completely distinguishing character which would enable any particular species to be maintained. Adult *G. clausa* vary in height from 11.5–19 mm and in diameter from 13.5–20 mm, mostly with $4\frac{1}{2}$ whorls. Unfortunately Sowerby's type of *clausa*, height 9 mm, diameter 11 mm, was a very small example and hardly typical of the species, even though size variation is considerable. It came from the Yemen, collected by Powys. Sowerby described it as 'depressedly orbicular' and noted that it was 'sometimes encircled by a single red band' (Sowerby 1847, p. 128).

The shells from Kathiawar were, in our opinion, correctly referred to *R.(S.) clausa* by Benson (1859) and their description as a new species, *C. hinduorum* by Blanford (1864) unjustified. Blanford claimed that the Indian shells differed in being much smoother, a feature not borne out by the numerous topotypes we have examined. It may be that Blanford saw too few Arabian specimens to realise just how much this species varies in strength of sculpture, height of spire and size. The type of *hinduorum* measured 11 mm high and 12 mm in diameter. The occurrence of the shells in India may well be accounted for by human introduction from Arabia.

Bourguignat's species *yemenica* was claimed by its author to differ from *clausa* in its smaller size, more convex spire and rounder aperture, but a completely circular peristome is a feature of the latter species and attention has been drawn to this feature by the authors of all the species which we have placed in the synonymy of *R. clausa*. Bourguignat likewise mentions a single yellow band, but this is in fact mentioned in the description of *clausa* as well as in those of *hadramautica* Melville and Ponsonby and *O. littlei* Pallary. In fact, the last two species differ from typical *clausa* only in respect of their greater size and both can be matched against material obtained by P. Cambridge at Salala, south Arabia.

G. pulchella Pallary is based upon a rather depressed example of *clausa*. It is said to be from Socotra, but nothing resembling it is otherwise known from the island and, although Pallary (1925a, p. 232) found himself unable to contest the locality, this is exactly what he should have done, since it is almost certainly erroneous. Arabia is the probable source.

We have also included in the synonymy of *R. (S.) clausa* imperforate species *O. dhofarensis* and *O. consimile*. The former is based upon three dead and bleached specimens, the latter on just two examples, one juvenile. We have examined paratypes of both and are of the opinion that they are both *clausa* in which the extension of the parietal callus across the perforation has not entirely covered it. In fact it may well have been broken away after death as would appear to be the case in the paratype of *dhofarensis* in particular.

W. H. Benson (1859, p. 2) described the living specimens of *R. (S.) clausa*: '... in *O. clausum* the foot is moderate in length and composed of two long narrow parallel soles separated by a deep sulcus, and having also a deep sinus between them at either end. The muzzle is greatly elongate, emarginate in front; and the lateral lobes are capable of considerable extension. The tentaculæ are moderate, hyaline, ringed, tumid and obtuse at the extremity. The eyes are prominent on the outer side of the tentaculæ near their base, not sessile on the head.'

On Benson communicating to W. Theobald a remark on the peculiar sole of this animal, Theobald stated that he had noticed it and that its use was to enable the species to cling to thin stems of the branches of the shrub which it frequents near the shores of Gopnath Point on the Gulf of Cambay. The leaves which he forwarded were examined by Sir W. Hooker who pronounced them to be those of *Grewia betulifolia* de Cand., an inhabitant also of Arabia whence Sowerby's type specimens of *C. clausum* came.

Benson also noted that by holding the living *O. clausum* in his hand for a few minutes and thereby imparting warmth to the animals, they were induced to come out and show themselves; the shells had been shut up for a year and had left Kittiwar eighteen months previously. From these observations it is apparent that the species is capable of living for considerable periods without food or moisture and could therefore well have survived a journey from Arabia to northwest India where, as we have suggested, it was probably introduced. Blanford (1864, p. 264) states that the climate of this part of India shows a certain approximation to that of Persia and northeast Africa, being on the margins of the area of periodical rains occurring in India and southeast Asia generally.

Plate 8 (opposite)

Figs. 1-2. *Revoilia (Socotora) clathratula* (Récluz). 1. Socotra $\times 2$. 2. Socotra Ras, Karma. North Coastline Plain (I. B. Balfour leg.) $\times 1$.

Fig. 3. *Revoilia (Socotora) guillaini* (Petit). Somalia, Halin Camp, $9^{\circ} 05'N$, $48^{\circ} 35'E$ (C. F. Hemming leg.) $\times 1$.

Figs. 4-5. *Revoilia (Socotora) guillainopsis* (Bourguignat). Somalia, Garbauen $\times 2$.

Fig. 6. *Revoilia (Socotora) naticoides* (Récluz). Socotra $\times 1$.

Figs. 7-8. *Revoilia (Socotora) albicans* (Sowerby). 7. Socotra $\times 2$. 8. Socotra, Dahamia (Forbes leg.) $\times 1$.

All specimens in the collection of T. Pain.



REVOILIA (SOCOTORA)



Plate 9

Revoilia (Socotora) bentiana (Melville 1885) Plate 2, figs. 2-3.

- 1895 *Otopoma bentianum* Melville: 224, pl. 14, fig. 8.
 1925a *Arabia bentianum* (Melville), Pallary: 225, pl. 35, fig. 8.
 1925a *Arabia bentianum* var. *daliyana* Pallary: 226, pl. 35, figs. 4-5.
 1925a *Arabia lucida* Pallary: 226, pl. 35, figs. 11-13.
 1960 *Otopoma (Arabia) bentiana* (Melville), Verdcourt: 223.

This species is confined to south Arabia and the type locality is a plateau in the Hadramaut, 400 miles east of Aden. Type material of *bentiana* is in the British Museum, Natural History, London and of *lucida* in the Dautzenberg collection, Brussels Museum.

Adult shells were found to vary from 13.5-16.5 mm in height and 17-22 mm in diameter, with between $3\frac{1}{2}$ and $4\frac{1}{2}$ whorls.

Comparison between the paratypes of both *bentiana* and *lucida* seen, leave us in no doubt that they are identical. Pallary (1925a, p. 226) claimed that *lucida* could be distinguished from the other by its greater size and more depressed form. Differences in size in this genus mean nothing and both are equally depressed. The aperture is circular, fully as high as wide, and the outer lip sharply reflected but not thickened. Its noticeably depressed form and reflected lip separate this species from the *clausa* complex, in which the shells are always distinctly more conical. We have not seen any intermediate examples in the material examined.

INCORRECT ATTRIBUTIONS

- Otopoma turbinatum* Godwin-Austen, 1881 (= *Cyclotropis*)
Cyclostoma radiolatum Martens, 1881 (= *Cyclotropis*)
Otopoma blennus Benson, 1859 (= *Pollicaria gravis* Benson juvenile).
Ligatella cecionii Bacci, 1851 (= ?*Revoilia guillaini* (Petit) no specimens seen).

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Plate 9 (opposite)

- Fig. 1. *Revoilia (Socotora) balfouri* (Godwin-Austen). Socotra, east end at 700 ft (215 m) (J. B. Balfour leg.) $\times 2$.
 Figs. 2-3. *Revoilia (Socotora) bentianum* (Melville). 2. Aden $\times 2$. 3. South Arabia, Makalla $\times 2$.
 Figs. 4-5. *Revoilia (Socotora) auriculare* (Griffith and Pidgeon). ?Socotra. 4. $\times 1$. 5 $\times 2$.
 Fig. 6. *Revoilia (Socotora) clausa* (Sowerby). South Arabia, Salala (P. Cambridge leg.) $\times 1$.
 Fig. 7. *Revoilia (Socotora) conica* (Godwin-Austen). Socotra, Gollonsir (I. B. Balfour leg.) $\times 2$.

All specimens in collection of T. Pain.

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REVIEWS

The Biology of the Mollusca. R. D. Purchon. 2nd edition. xxv + 560 pp. Pergamon Press, Oxford & New York. 1977. Price £17.50.

This book attempts to review all the papers on the biology of the Mollusca published in the last half century. Such a vast task has been accomplished by limiting the search primarily to English language sources, and the content to separate, almost isolated topics which the author considers important and with which he is familiar.

The initial chapters discuss the contribution of the mantle cavity, its associated organs, buccal mass and radula to the great diversity of feeding mechanisms and mode of life, especially in the gastropods and, where appropriate, the bivalves. The adaptive radiation of the polysyringian (filter feeding) bivalves is particularly explored with a functional and descriptive comparison using a simple Glycimerid model. Succeeding chapters include a comprehensive review of the problem of digestion, reproduction, including all functions involved in the successful replacement of generations from courtship to larval behaviour, and different aspects of distribution, e.g. geographical isolation, intertidal zonation, intra-specific variation of *Cepaea* and some interesting occurrences of passive redistribution. The final chapter on the Cephalopoda emphasizes their unique adaptation to a free swimming, carnivorous mode of life and their highly developed nervous system.

The two appendices, which comprise nearly a quarter of the book, deal with the biology of the molluscan classes; the Monoplacophora, Polyplacophora (Chitons), Aplacophora, Scaphopoda (Tusk shells) are described briefly, whereas the Gastropoda, Bivalvia and Cephalopoda are dealt with in the style of a dissection guide. The 'typical' species although being widespread, easily available and not difficult to dissect, are specifically chosen for their unfamiliarity, so that dissection is not 'automatic', but comparisons can be made with other species as exemplified by a questionnaire. Each section on the major classes closes with a useful table of the classification used and references to the species mentioned in the text.

Much thought has gone into the layout of the book; intelligent use is made of subheadings, which are listed in the table of contents, and each chapter is preceded by a detailed synopsis and closed by references which, in all, number about 600. The copious illustrations are taken, wherever possible, from the original papers and are accompanied by detailed self-explanatory captions, uncluttered by keys to notations which appear at the end of each chapter.

This is the 2nd edition of a work which despite the intervening 10 years since its first publication, includes only 6 new papers, one of which does not appear to be referred to in the text, covering bivalve feeding, digestion including possible environmental and behavioural cyclical patterns, the development of the carnivorous mode of life in the Verticordiidae (Bivalvia), and the distribution of terrestrial molluscs on Pacific islands. The book has remained substantially unchanged, including the now incorrect list of figures for the 1st edition, whereas unfortunately the price has not. It does however continue to be a commendable and advanced introduction which brings into perspective aspects of the biology of the classes which compose the phylum Mollusca.

PETER F. LINGWOOD

Natural History Auctions 1700–1972. A Register of Sales in the British Isles. Compiled by J. M. Chalmers-Hunt. London: Sotheby Parke Bennet 1976. xii + 189 pp. £15.00.

This book is an unique attempt at a complete list of Natural History Auctions in Britain between 1700 and 1972. The only comparable works are Tomlin's '*Shell Sales*', which deals exclusively with conchological collections and Sherbourne's '*Where is the . . . collection?*' which, although including many sales, was intended more as a guide to the present location of collections. In any event, only 500 copies of the latter were printed privately in 1940, so that it is not only scarce but out of date.

The collection of natural history objects, although often haphazard and without sufficient regard to provenance, has contributed enormously to the advancement of scientific knowledge. Details of sales enable the tracing of historic cabinets and through the sale catalogues, rare and important individual specimens. These catalogues may also, if illustrated, be aesthetically pleasing, and some, notably Solander's Catalogue to the Duchess of Portland's Sale in 1786, because of the early application of binomial nomenclature, are taxonomically important in themselves. It is from these catalogues that Chalmers-Hunt draws his information, as happily and perhaps surprisingly many remain extant, despite their ephemeral nature.

The book itself is divided into two parts; 48 pages of introductory articles by seven different authors and 127 pages of the register itself compiled by Chalmers-Hunt. These authors (J. M. Chalmers-Hunt, insects; A. C. Wheeler, vertebrates except birds; W. T. Stearn, plants; C. Simpson, birds and eggs; W. D. I. Rolfe, fossils; P. G. Embrey, minerals; S. P. Dance, shells), attempt to place the sales in perspective. Their treatment varies in approach and depth, and some are obviously struggling to fill their allotted pages. These could have been supplemented if not replaced by histories of some of the more important auction houses. However the best of the articles provide, for those unfamiliar with the subject, a fascinating insight into the fluctuations in collecting.

The most frequently advanced explanation for the popularity of a particular item is its aesthetic appeal or otherwise, although undoubtedly the durability and the inadequacy of preservation techniques were important factors. In general however, natural history collecting in Britain became popular during the 18th century when the possession of a cabinet became almost a social necessity. The quality of these varied from the purely decorative, through the purely acquisitive to the scientific; their fate depending on the owner's continued interest or that of his heirs. Fortunately, the collections of the more discriminating were either offered intact to institutions or fellow collectors, or were auctioned publicly.

The importance of the sales followed the rise in collecting, reaching its peak in the latter half of the 19th century. The subsequent decline of both was a result of the diminution of personal fortunes and accompanying leisure, and also the corresponding increased expense of collection and curation. The exception to this general trend was the collecting of insects, which reached its apogee at the beginning of this century. Some aspects, however, never recovered from the decline, because of subsequent legislation, e.g. the Protection of Birds Act, or modern technology, e.g. hindering the collection of minerals, although the enforced travel of the Second World War, renewed appreciation of Victoriana and the desire to counteract inflation has rekindled interest, especially in shell collecting.

The second part of the book, the register itself, tabulates nearly 1500 sales chronologically, so that together with the collector index (which refers to both sections) one can locate the sale from its date or the collector's name or perhaps the year of his death. The Sale date is followed by the collector's name and his residence, if known, and the contents of the collection divided into 28 categories. This is followed by the auctioneer, the location if not in London, the number of lots, pages and illustrations in the catalogue. This information should satisfy the casual enquirer, but for the more serious, the repositories (69 in all) of all the known catalogues are listed together with the extent of annotations. This eliminates some unnecessary correspondence, and indirectly, and perhaps more importantly, ensures the continued preservation of catalogues through consultation and copying.

To save space and repetition, many of the details are extensively abbreviated; these are not always self-explanatory and might be confusing, e.g. col. = coleoptera, coll. = collection, though they are all clearly keyed.

Shells are the most frequently auctioned item (approximately half of all collections sold contain some at least), so the conchologist gets the greatest value for money from this book, although paradoxically he is already the best served. (e.g. Dance 1966, Tomlin 1942-9). Neither of these works could be considered to replace Chalmers-Hunt's book, although the former perforce makes the brief introductory article somewhat redundant to the owner of both.

It should be remembered, when using this book, that by no means all the collections were auctioned and that if they were, it was not necessarily in the British Isles. This book does, however, mark the extent of our present knowledge and although it cannot and does not claim to include all auctions, I would be surprised if many more were found. It would be tempting to suggest that the generous format was provided for these additions, but it is probably to justify the high price (which appears to have increased by £2.50 since publication) of a book with unfortunately limited appeal. I hope that its very publication will stimulate interest in recording natural history sales and the current whereabouts of collections, and I confidently expect to see it appear on the bookshelves of many natural historians.

- DANCE, S. P. 1966. *Shell collecting: An illustrated history*. Faber & Faber, University of California Press. 344 pp.
 SHERBOURNE, C. D. 1940. *Where is the . . . collection?* Published at the author's own expense.
 TOMLIN, J. R. le B. 1942-1949. *Shell Sales (I-VI)*. *Proc. malac. Soc. Lond.* **24**: 157-160; **25**: 25-33, 96-99; **27**: 254-256.

PETER F. LINGWOOD

British freshwater bivalve Mollusca. Synopses of the British fauna (New Series) No. 11. By A. E. Ellis, 109 pp., 15 pls., 39 text-figs. Linnean Society and Academic Press. 1978. Price £2-80.

This synopsis has a long previous history and will be thoroughly familiar to most members of the Society. It began as a series of three separate papers, on *Pisidium*, *Sphaerium* and the unionid mussels, first published in the 1940s. These were then revised and brought together in 1962 (as the old series synopsis No. 13) and now, again revised and updated, it has reappeared. This long history is a tribute to the usefulness of Mr. Ellis's work and his synopses have been very much in demand over the past 35 years or so. For those unfamiliar with the work, it provides a concise and up to date account of all the British Pleistocene and Recent non marine bivalves. The inclusion of fossil forms has undoubtedly contributed to the demand for this synopsis, which contains in one small handbook keys, figures and photographs to aid the identification of all the British freshwater mussels.

REVIEWS

A major interest in the reissue of a familiar work is to see what changes have been made. Mr. Ellis modestly states on p. 2 that the chief changes are the omission of descriptions of named varieties, a drastic curtailment of the bibliography and the addition of a section on the structure, mode of life and reproduction of freshwater bivalves. However, other changes, especially in the layout, have been made, which I think improve the usefulness of the synopsis.

The omission of varieties is welcome. Details of variation are still included, particularly the '*ponderosum*' and '*pseudo-sphaerium*' variants of some pisids. Researchers on freshwater bivalves will miss the detailed bibliography included in the old series (which will ensure it a continued place on library shelves), but this does not detract seriously from an identification handbook. On the subject of identification, a most useful feature of the new synopsis is the positioning of the line illustrations within the text and not grouped together at the end as in the previous issue. No longer does one have to read the descriptions of possible species and then search for the appropriate figures, which I found particularly time consuming when trying to identify my pisids. Furthermore, there are new line drawings of *Corbicula fluminalis*, *Sphaerium solidum* (found living in Britain since the previous issue was published) *S. dickinii* and *Pisidium clessini*, as well as those accompanying the new section of text. The umbonal appendicula and hinge callus, key features in the identification of some species of *Pisidium*, are labelled directly on the drawings; another improvement. Two photographs of a recent specimen of *S. solidum* replace one of the fossil examples, formerly illustrated, but otherwise the plates are reproductions of the originals with new lettering and a new order. One or two plates have lost a little definition compared with the previous issue, but they are still generally very good.

The new text, pp. 3-13, is a very useful summary of morphology, anatomy and reproduction and includes illustrations of the veliger larva of *Dreissena* and the glochidium of *Anodonta*, among others. This section serves as a useful introduction for those interested in more than just identifying their material. Altogether this is an excellent synopsis, improved considerably by its revision and will, I am sure, prove most useful for many years to come.

C.R.C.P.

THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND
INCOME AND EXPENDITURE ACCOUNTS FOR THE YEAR ENDED 31st DECEMBER 1977

	£	£	£
Publications:			
News Letter...
Student Papers
Paper for Students Papers Bought in Advance..
	82.52	1,251.38	2,557.81
	135.99		1,305.71
			32.00
		218.51	3,895.52
Journal:			108.39
Volume 29 No. 3
Volume 29 No. 4
	982.18		...
	1,139.95		824.77
		2,122.13	40.00
			67.54
			62.62
			13.27
			12.90
			1,021.10
Cost of Atlas, Postage and Packing...	...	145.25	
Printing, Stationery and Postage	...	496.41	
Officers' Expenses	...	165.92	
Subscriptions	...	12.00	
Meetings	...	30.90	
			732.56
			202.66
			109.57
			1,044.79
			109.57
			935.22
			£5,960.23

BALANCE SHEET AS AT 31st DECEMBER, 1977

Fees and Subscriptions in Advance ...	£	491.88	Cash in Hand:	£	2.08
Life Membership Fund	1,810.00	Cash at Bank:	...	405.29
Reserve and Research Fund	1,088.20	Current Account	...	551.98
			Deposit Account	...	3,509.68
			Post Office Savings Bank	...	4,469.03
<i>Capital Account</i>					
Balance Brought Forward ..	6,542.74				
Add Surplus for the Year ...	1,517.73				
		8,060.47	<i>Investments</i>		
			£400 5% Treasury Stock 1986/89	...	344.00
			£500 5¾% Deb. Stock Mersey Docks & Harbour Board 1980/82	...	222.29
			2,514 Units M. & G. Dividend Fund	...	1,522.06
			£400 12½% Loan City of Norwich	...	400.00
			£800 5½% Loan London County Council	...	769.20
			1,620 Scotincome Units	...	892.95
			£875 7% Deb. Stock 1978/83	...	753.82
			£500 Manchester Corporation	...	500.00
			£700 Bury 12¼% Loan	...	700.00
			£800 15½% Treasury Stock 1998	...	768.00
			£98.80 Subordinated Loan Stock Mersey Docks & Harbour Board	...	98.80
			104 10p Ordinary Shares Mersey Docks & Harbour Board	10.40
		£11,450.55			6,981.52
					£11,450.55

MARJORIE FOGAN,
Hon. Treasurer.

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L. LLOYD-EVANS
W. F. EDWARDS

27th February, 1978

Hon. Auditors.

PROCEEDINGS OF THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND

TREASURER'S REPORT, 1977

The accounts for this year show that the Society has been very successful in holding its own. Members' Subscriptions and those of Subscribers both show a gratifying increase, although there is a slight fall in the income from Covenanted Subscriptions since a number of Seven Year Covenants have expired; the Society would be grateful if more Members would sign Covenants for the payment of their Annual Subscriptions.

The *Atlas* has again provided a substantial income, and it is hoped that this will continue to sell for some time to come; it is gratifying that it has enjoyed a considerable sale overseas.

Most of the usual costs—publications, postage etc.—have, as usual, shown an increase, but a considerable economy was achieved in the costs of the *Journal of Conchology*. The Society has considered it prudent to lay in an advance stock of paper for *Papers for Students* at an advantageous price.

The investment income shows the benefit of the new investments made in 1976. It is hoped to make a further increase in our holdings in 1978.

21 Members and 11 Junior Members are in arrears with 1977 Subscriptions. All Members are reminded that no further publications can be sent to those whose current Annual Subscriptions remain unpaid.

Unfortunately I am obliged to report that in 1977 there were considerable difficulties with the post; a number of items of correspondence were lost and these regrettably included several remittances. Should any member who has sent a cheque (or P.O.) in payment of his Subscription receive a reminder from me, I beg that he will check that it has indeed been cashed.

MARJORIE FOGAN,
Hon. Treasurer

REPORT OF THE COUNCIL, 1977-78

Membership. It is with regret that the Society has to report the deaths of the following Members: Rev. G. K. Wrigley, who joined in 1964; Mr. H. Knudsen, who joined in 1960; Mr. E. Robinson, who joined in 1954. Total membership now stands at 612 Members, comprised of the following categories: Full Members—534, of whom 28 are Life Members and four Honorary Members; Family Members—43, of whom five are Family Life Members; Junior Members—35. During the year a total of 59 new Members joined the Society, including nine Junior Members. 23 Members resigned and 25 were struck off for non-payment of subscriptions.

Subscribers. There are 176 subscribers to the *Journal of Conchology* and 11 subscribers to the *Conchologists' Newsletter* and *Papers for Students*.

Meetings. Six ordinary meetings and one annual general meeting were held in the Conversazione Room at the British Museum, Natural History, as follows: 16 April 1977: Conversazione meeting. 21 May 1977: Lecture 'Non-marine molluscs in Wales' by Dr. June Chatfield. 22 October 1977: Lecture 'Some early ideas on Geology and Fossils' by Mr. R. A. Martin. 19 November 1977: Lecture 'Something different' by Mr. S. P. Dance. 17 December 1977: Lecture 'The genus *Neptunea* in the North Atlantic' by Mr. T. Pain. 21 January 1978: Lecture 'Collecting marine molluscs in the Hong Kong area' by Mr. J. Orr. 17 February 1978: Lecture 'Snails under the microscope' by Mr. R. Preece. 18 March 1978: Annual general meeting: Presidential Address 'The evolution of the conchologist' by the President, Mr. P. E. Negus.

Field meetings. Eleven field meetings were held during 1977 as follows: 13 March, Brighton, Sussex. 20 March, Beachy Head, Sussex. 28 April, West Runton, Norfolk. 14 May, Camber Sands, Sussex. 28 May, Leicester. 2-3 July, joint meeting with the Yorkshire Conchological Society. 23 July, joint meeting with the Ipswich Geological Group. 28 August, Windsor, Berks. 18 September, joint meeting with the Northamptonshire Natural History Society. 15-16 October, Bridlington, Yorks. 28 October, Farleigh Down, Surrey.

Thanks are due to the following for leading these meetings: Mrs. M. Maddrell, Mrs. C. J. Pain, Dr. A. J. Rundle and Messrs. P. Cambridge, I. Evans, D. Holyoak, R. A. D. Markham, A. Norris, G. Osborn and D. R. Worth.

Publications. Two parts of the *Journal of Conchology* were issued, volume 29, parts 3 and 4 as well as the quarterly *Conchologists' Newsletters*.

PROCEEDINGS

RECORDER'S REPORT: NON-MARINE MOLLUSCA

A. GRID MAPPING

A new field recording card was published by the Society early in 1978, to replace our well-known card which has done duty since 1961. The Society gratefully acknowledges a grant from the World Wildlife Fund to pay for the printing. The list of species has been revised in accordance with the nomenclature used in the *Atlas* and in the check-lists published in *J. Conch., Lond.* **29** (1976): 21–28. A new instruction leaflet has also been prepared to accompany the card.

A set of twelve transparent overlays for the *Atlas* showing vice-counties, climate, geology, etc. has been published by the Biological Records Centre. Copies can be purchased through the Society (see *Newsletter*).

In September a Conchological Society party made a very successful mapping expedition to Ireland. Coverage for hitherto little-explored tracts in the central plain and in the south-west was substantially improved.

B. VICE-COUNTY RECORDS

The following new records have been verified since the last Report (*J. Conch., Lond.* **29**: 229). Unless stated otherwise, the date of collection was 1977–78. Where no collector's name is given for an Irish record, this was made during the course of the Society's summer mapping expedition; the members of the party were Mrs. M. Fogan, Mrs. E. B. Rands, Mrs. H. C. G. Ross, R. Anderson, M. P. Kerney and R. C. Preece.

Bedford (30): *Abida secale*, Whipsnade (42/9918), B. S. Nau.

Worcester (37): *Acicula fusca*, Eastham (32/6767), R. C. Preece.

Leicester (55): *Sphaerium transversum*, Grand Union Canal, Kilworth (42/6284), J. H. Mathias.

York North-east (62): *Truncatellina cylindrica*, Scarborough (54/08), A. Smith, 1921 (Leicester Museum).

York Mid-west (64): *Succinea oblonga*, Asselby Island, Goole (44/7626), B. Coles.

Cheviot (68): *Planorbis carinatus*, Swinhoe Lake (46/0735); *Pisidium hibernicum*, Hetton Lime Lake (46/0235), both A. Walton.

Kirkcudbright (73): *Ashfordia granulata*, Nether Clifton (25/9156), L. Lloyd-Evans.

Aberdeen North (93): *Planorbarius corneus*, Pitfour Loch, Old Deer (38/9748; probably introduced 'about 40 years ago'), M. W. Young.

Limerick (H 8): *Oxychilus helveticus*, Broadford (R 3123); *Pisidium obtusale*, Pallaskenry (R 3854); *Pisidium hibernicum*, Patrickswell (R 5451).

Tipperary North (H 10): *Deroceras caruanae*, Rear Cross (R 8459).

Offaly (H 18): *Milax budapestensis*, Edenderry (N 5930); *Cochlodina laminata*, Clonad Wood, Tullamore (N 3119); *Anodonta anatina*, Grand Canal, Ferbane (N 1122).

Kildare (H 19): *Ancylus fluviatilis*, Kilcullen (N 8709); *Spermodea lamellata*, Ballyvass Wood, Kilkea (S 7587).

Wicklow (H 20): *Semilimax pyrenaicus*, Humewood Castle, Kiltegan (S 9386).

Westmeath (H 23): *Acanthinula aculeata*, *Spermodea lamellata*, Tudenham Park, Lough Ennell (N 4146); *Testacella scutulum*, Ballynagore (N 3539).

Fermanagh (H 33): *Anodonta anatina*, Camagh Bay, Lower Lough Erne (H 1553), R. Anderson.

Donegal East (H 34): *Acroloxus lacustris*, Lough Numman (G 9372); *Cerņuella virgata*, Rossnowlagh Strand (G 8568), both R. Anderson.

Tyrone (H 36): *Vertigo substriata*, Lough Bradan (H 2572); *Semilimax pyrenaicus*, Knockmany Forest, Augher (H 5456), both R. Anderson.

The most noteworthy discovery is that of *Oxychilus helveticus* in Ireland (see *J. Conch., Lond.* **29**: 261). Other interesting Irish finds, representing considerable extensions to known ranges, are *Cochlodina laminata* in an old mixed deciduous wood in Co. Offaly; *Semilimax pyrenaicus* in Co. Wicklow (see *Ir. nat. J.* **19**: 170) and in Co. Tyrone; *Anodonta anatina* in Co. Fermanagh; and *Cerņuella virgata* in Co. Donegal.

Among the British records, the most interesting is Dr. Coles' discovery of *Succinea oblonga* in marshy woodland on an island in the River Humber. The identification was checked by dissection.

M. P. KERNEY

RECORDER'S REPORT: MARINE MOLLUSCA

A. RECORDING

Progress during 1977 continued at a steady rate in most areas, but the Underwater Conservation Year had a considerable impact on a few areas. The concentrated efforts of off-shore divers invariably increased the number of records of molluscs and particularly those of the nudibranchs. For example, Mr. B. E. Picton, diving in the North Cornwall Area 20, produced 14 records of nudibranchs new to the area, and one new to science.

Mr. M. Brisco completed his first year as area representative for the newly created 29a, Antrim, which was

separated last year from 29, Clyde and Argyll. Starting almost from scratch he gathered, mostly by his own unaided efforts, 430 records consisting of 144 species, 41 of which were 'live' records. Considering that Mr. Brisco is currently involved with studies and examinations, this is a splendid effort.

Reports were received from 8 areas totalling 169 new records, and many upgraded ones. The following new area records were received:

Area 29a. Starting from scratch, virtually all of M. Brisco's 430 records of 144 species are new to the area.

Area 16. The opisthobranchs *Coryphella verrucosa*, *Embletonia pallida*, *Limapontia depressa*, *Tergipes tergipes*, *Trapania pallida*, and *Trinchesia foliata* are new area records.

Area 19. *Acteonia senestra* is a new record for the Scillies.

Area 20. The opisthobranchs *Doto millbayana*, *Coryphella pedata*, *Facelina auriculata*, *Coryphella lineata*, *Polycera faroensis*, *Ancula cristata*, *Facelina curta*, *Limacea clavigera*, *Lomanotus genei*, *Trinchesia foliata*, *T. plebia*, *T. caerulea* are new area records.

Area 2. *Littorina mariae*, *Eubbranchus farrani*, *Glossus humanus*, *Lutraria angustior* and *Sepia officinalis* are new area records.

Although 10 km master cards were sent, soon after request, from areas 2, 11, 14, 15, and 29, no more were sent during 1977. Until the marine Recorder has copies of 10 km masters he, or she, will not be able to judge when we are ready for atlas production. Please gather your shore records into 10 km master cards and send copies to the Marine Recorder as soon as possible.

B. CHANGES

The following changes have taken place:

- 1) Miss Mary Milne has retired after many years of hard work in Area 2 Solway, and her place is taken by Mr. Norman Hammond (address, 39 Outgang Road, Aspatria, Carlisle, Cumbria). We thank Miss Milne for all her efforts and extend greetings to Mr. Hammond.
- 2) Dr. Peter Lingwood, Area 24 Liverpool Bay, formerly at Merseyside County Museums, is now at 3 Min-y-Brenig, Pentre-llyn-cymmer, Cerrigydrudion, Nr. Corwen, Clwyd LL21 9TT.

For a variety of reasons I have resigned from the post of Marine Recorder, although I will remain in office until the end of the year when a successor, chosen by Council, will take over. It is my hope that the suggested policies, aims and plans, outlined in the Marine Census articles, will continue to serve as a flexible basis for progress in the marine census. Please accept my thanks for your cooperation, and my best wishes for a 'speedy atlas'.

C. P. PALMER

JOURNAL OF CONCHOLOGY

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CORRECTIONS

Page

- 25 List of species: for **Opeas pumilium* read **Opeas pumilum*.
- 122 Line 11 from foot: for *Tritonia plebeia* read *Tritonia hombergii*
- 259 Second line of acknowledgements: for Dr. J. Hatfield read Dr. J. Chatfield.
- 277 Foot of table 3: for P 0.05 read $P > 0.05$

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